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ECOLOGY

A QUARTERLY JOURNAL
DEVOTED TO ALL PHASES OF ECOLOGICAL BIOLOGY

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By H. GODWIN

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This number of *ECOLOGY* is dedicated to the memory
of
BURTON EDWARD LIVINGSTON

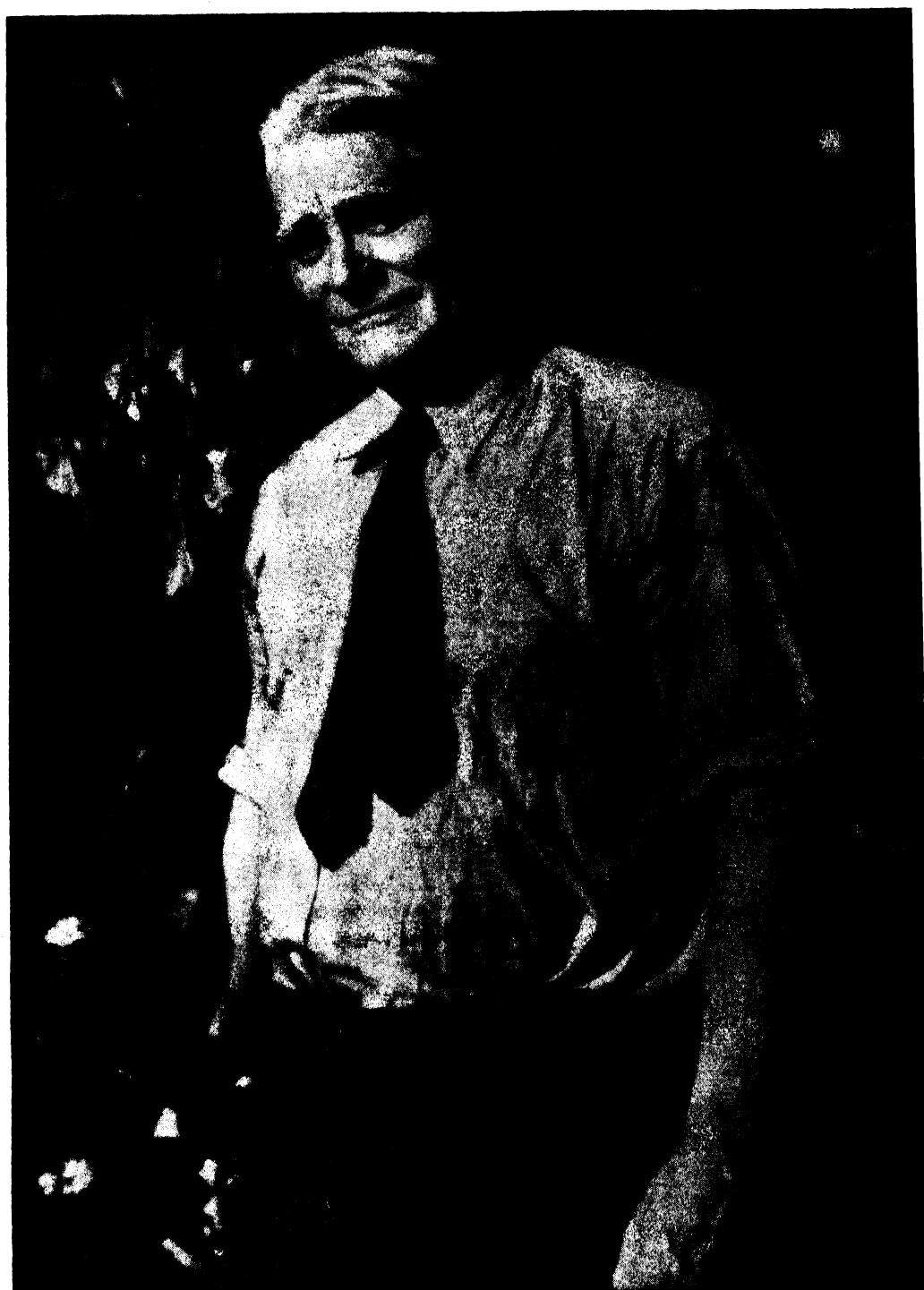


FIG. 1. Burton E. Livingston in his garden at Riderwood, Maryland, August 21, 1944.

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JULY, 1948

No. 3

SOME CONVERSATIONAL AUTOBIOGRAPHICAL NOTES ON INTELLECTUAL EXPERIENCES AND DEVELOPMENT: AN AUTO-OBITUARY

BURTON E. LIVINGSTON

INTRODUCTION

(By D. B. Lawrence)

This issue of *ECOLOGY* is dedicated to the memory of a very influential worker in the field of "physiological ecology," Dr. Burton E. Livingston, who died February 8th. Livingston was for many years in charge of the Laboratory of Plant Physiology and occupant of the Chair of Forest Ecology at The Johns Hopkins University. Since his retirement in 1940, he had carried on his research at his home in Riderwood, Maryland. He probably will be remembered best by ecologists for his contribution in atmometry,¹ "Atmometers of porous porcelain, and paper, their use in physiological ecology," published in *ECOLOGY* in 1935, and for his publication with Forrest Shreve "The distribution of vegetation in the United States, as related to climatic conditions," but his contribution to physiological ecology was spread widely over the field of water relations and mineral nutrition of plants. His viewpoint was outstandingly ecological and he conceived of the environment as something which had an inherent capacity to *supply* materials and energy to the dynamic organism, and also to *remove* materials and energy from an organism. He went to great lengths to devise instruments which

would measure the rates at which the environment supplied materials such as water and oxygen, and rates at which the environment removed material such as water from the plant. He planned his research in mineral nutrition, always with an ecological background which included the fluctuating regimes of light, temperature, and humidity inherent in the greenhouse conditions at Baltimore. He was not satisfied with constant conditions of environment nor with conditions at any one season of the year so he would repeat experiments four times or more to cover the various seasons. Nor was he satisfied with standard greenhouse bench experimentation which introduced tremendous differences in microclimatic influences; nothing short of a tremendous rotating table with flowing solutions, and using very carefully selected plants, chosen not only for uniform genetic background but also uniform physiological response, made him feel content. Livingston was one of the first to carry physiological methods into the field, and to him ecology is greatly indebted for pointing the way to improvement in method and viewpoint. Probably Henrik Lundegardh is the only other person who can compete with him for top credit in welding physiology and ecology together. Livingston had few prejudices, but he had one that was striking; he had no use for statisticians or

¹ Readers will be glad to know that the atmometer business which had long been operated on a world-wide scale by Dr. Livingston from his home in Riderwood, will be continued at the same address by Mrs. Livingston.

their methods and, so far as I know, he never went beyond the mean and the extremes in his mathematical analysis of scientific data. He felt that if there were important differences to be detected, they could be seen from a table of figures, and he felt that statistical treatment was too often used as a substitute for adequate planning and careful technique. His lack of appreciation of this field was as striking as Clements' blind-spot for genetics, and yet this did not deter his students from interesting themselves in that line. Indeed his antipathy toward statistics probably contributed strongly to making a student of his one of the U. S. Air Forces' top statisticians today.

Livingston's finest attribute, so far as student training was concerned, was the limitless energy and effort he devoted to the criticism of a manuscript. Each page was gone over orally, across the table, paragraph by paragraph, line by line, word by word, critically examining each expression to be sure that no ambiguity was left, and that there was not some more accurate way of expressing the idea. He devoted the same energy to answering letters from fellow scientists, and would often answer a query with a 10-page letter and the apology that he was sorry he didn't have time to write a short letter.

Livingston will always occupy an important place in the history of ecology because he played a vital role in directing ecological research toward precise measurement of the natural environment, and experimentation, during the formative years of the development of our field. It will be remembered that until the late 1800's ecologists, with the exception of Bonnier in 1890 and 1895, were content with superficial observations and untested hypotheses, and as late as 1893 the statement was propounded at the Madison, Wisconsin, Convention of Botanists that "ecology was *observational* and physiology *experimental*." Nothing could have been more stimulating to ecologists, and their minds seemed to explode with indignation, though to be sure, a long time-

fuse was very definitely attached which took 12 to 15 years to burn. Clements in 1905 was first in this country to respond. In the first chapter of his book "Research methods in ecology" he tried to show that there was essential identity of physiology and ecology and he thought that the two fields would become one and that the name would probably be physiology. Clements seems to have coined the term "experimental ecology" in the same chapter. He considered Bonnier (1890) the first to carry on ecological experimentation out of doors. In December 1908 at a Botanical Society symposium in Baltimore entitled "Present problems in plant ecology" Livingston was one of the five ecologists and physiologists who spoke their minds. All pointed out vigorously the need for precise measurement of environmental influences² and emphasized the fact that ecology could be experimental, and had to be if it was to advance to anything that scientists would mention without a smile. Almost immediately thereafter ecologists began applying experimental methods to the solution of ecological problems and this has brought forth fruit abundantly in the applied fields of forestry, range management, plant pathology, horticulture, and wildlife management. The year 1893 should therefore be considered the date of stimulus and the year 1905 (Clements) the beginning of the response that brought ecology close to the side of physiology, but it was the year 1908 and the ideas of Livingston, Cowles, Transeau, Spalding, and Shaw, that really set ecology and its applied phases off on a new tack with the recommended use of experimentation in the solution of problems.

It seems unnecessary here to list individually the publications that emanated from the Laboratory of Plant Physiology during Livingston's 31 years of active service as its chief, but a statement of the total production will reveal the energy

² Livingston would not use the word *factor* in this sense; he preferred to restrict its use to the mathematical sense.

of the man. In all, 269 articles were prepared for publication, and 30 students received their Ph.D.'s in that time. It is doubtful that any other person in the nation has ever demonstrated such a sustained high level of activity in this branch of science. It is not the purpose of this introduction to catalogue the scientific activities of this remarkable man. The intent here is to point out the unusual fortune of ecologists in having on record the following "auto-obituary" as Livingston jokingly called it when he submitted it to me at my request in November, 1937. It is important for us because it traces the ecological development of a very influential worker of our field of science during the critical early stages in its development.

THE AUTO-OBITUARY—NOVEMBER, 1937

My boyhood was spent in Grand Rapids, Michigan, where our home grounds were an unusually large town lot near the edge of the growing city, at the northeast corner of what are now Sheldon and First Streets. Across the street to the south was the shallow valley of a brook, which flowed through a treeless mucky stretch where grew mints and iris, Joe Pye weed, iron weed and milkweed, sedges and grasses. In other directions there were neighbors' homes and a few lots still vacant—remnants of upland meadows, where we "studied" bumble bees in one of my early summers, and red clover. The natural forest of this moraine edge was "oak opening," but there were few native trees excepting a patch of upland oak forest a block or two away. I think I was familiar with the burr oak and the white oak before I entered my fifth year. The other trees of my very early acquaintance had been planted, though most of them represented species native in that region. A few blocks to the west, in the broad valley of the Grand River and a tributary creek, there were railways and a variety of swampy stretches, where the river overflowed in spring. There were log jams

(white and Norway pine) in the 80's. I afterwards mapped that glacial topography in the paper on Kent County and described its natural vegetation after a fashion (BOTANICAL GAZETTE, 1903).

Our home lot was largely in cultivation, with little lawn. There were beds of vegetables, rows of Mexican blue maize and potatoes, beds and patches of native "wild flowers," currant and gooseberry bushes, grape vines on the "back fence," sumacs, tall tree-like sunflowers (*H. annuus*) for the chickens. Around the margins of that lot were large trees of sugar maple, silver and Lombardy poplar, elm, white cedar, red cedar (*Juniperus virginiana*), tamarack, butternut, sassafras, horticultural cherries and apples—both eating and crab. Two of the crab-apple trees had been so grafted that each bore three or four kinds and sizes of fruits, which ripened one after another. A single peach tree died before I became well acquainted with it. Almost all of the old-fashioned ornamentals of that region and period were abundant—tulips, hyacinths, croci, candidum lily, daffodils, gladiolus, English violet, primula, columbines, various ferns, vinca, euphorbia, perennial pea, flowering currant, lilacs, snowball, euonymus, roses, German iris, hollyhock, hibiscus, and many annuals. I was something of a specialist in growing pansies in rock-paved beds when I was about fifteen. In spring there were small flats of seedlings in the house, where there were always numerous "house plants" before the windows. We had an oleander, but no rubber plant. I suppose I planted the seeds of my two potted trees of orange and lemon at the age of four or earlier. They were inconveniently large before I went away and left them to whatever fate finally overtook them.

Perhaps one of the most influential portions of my botanical environment in very early years was our haphazard plantings of native flowering plants—spring flowers such as two hepaticas, bloodroot, Claytonia and the rest, two

yellow cypripediums, and so on; also the common weeds of the garden and roadside, like stellaria, polygonums, pigweed, amaranth, the smaller ragweed and others. The last-mentioned was esteemed in mid-summer as furnishing a convenient added weight for the end of a kite's tail. We called many of these plants by their Latin names; I am unable to recollect a time when I didn't recognize the two hepatica species of that region as triloba and acutiloba, but I think I had reached high-school age before I had any name at all for *Ambrosia artemisiaefolia*, and I have never called that kite-tail plant ragweed without feeling bookish and pedantic to a degree.

Perhaps I took naturally to plants and their ways, but parents and older brothers and sisters had been and were specially interested in plants, and to their interest was due the peculiar immediate environment into which I came, and those early surroundings gave what was going to become my mental and philosophical leanings an unusual bent towards the field of plant science. But there were other influences. My parents had grown up on farms and they had the usual knowledge and interests of farmers, but we lived in town and my father had become a street-grading and sewer contractor for the rapidly growing community. In his business he dealt with soil and gravel and paving stones, with sand traps, gutters and gravelled road surfaces, with pick-and-shovel workers and teamsters, with plows, scrapers, paving hammers and an iron road roller that was drawn by a team of horses. He paved several long stretches of streets with cedar blocks, with coal tar poured into the joints, but I am sure he never saw a street paved with brick or asphalt or concrete; those things came later. My boyhood surroundings therefore included the grading contractor's equipment; tool boxes, of shovels, picks, saws, hammers, canthooks and such, came home in the fall, to remain in our backyard till they went out onto the "jobs" the following spring. My earliest memories are framed

with tools of rusty iron, plows, scrapers and the interesting contents of those old tool boxes. The red-chimneyed kerosene lanterns were of special interest.

In those days, in that region, street grading and paving was all accomplished in summer and my father was at home most of the time in winter. In that season the tools were repaired for use the following summer. My father and older brothers were experts at the hand wood-work of these operations, and I cannot remember when I was not familiar with saws and planes, with draw-shaves and spoke shaves, with bolts and screws and nails, with wrenches and files. In my time we never had a forge, but I played about an ingenious shaving horse, which held the work when an axe handle or pick handle was being shaped from selected pieces of hickory wood. It is thus seen that my boyhood surroundings extended into the realm of simple mechanical operations as well as into that of gardening and plant lore.

Still another feature of those early surroundings lay in a home atmosphere of books, reading and ideas. There were many books about the home and they continually increased in number. There were generally a number of books from the public library. Every one in the family circle read and read. We had the complete file of Harper's Magazine and the subscription was always continued; for a number of years we had the old Century Magazine. Beginning when I was seven I read the St. Nicholas magazine pretty thoroughly for the next four or five years. The "big dictionary" (Webster's unabridged) was in plain sight on a table in our living room, and it was used almost every day. I think my first use of it was to elevate a chair seat when I sat at that table to play with letter cards, author cards, jack-straws or checkers. I became acquainted with the names of many literary personages and their pictures, also with their main titles, from that old game of "authors." We were never much interested in ordinary playing

cards, whose peculiar attractiveness has always been far beyond my mental capacity. Longfellow and Bryant were my first poets. From having them read to me, I knew by heart many of their passages before I was able to read. I attended a Congregational Sunday school regularly for many years, finally ceasing when the teacher of my class left town. Though some of the older brothers and sisters attended that church, I never cared for that popular sort of recreation, and my reading of the Bible was generally confined to the preparation of each Sunday-school lesson. I never knew either of my parents to attend church. Life flowed smoothly in our group, without the common religious precepts. I remember a few experiments with prayers when I was very young, but they always gave negative results. Only when a ministerial relative—of whom there were many, it seems—came to our home did I hear grace said at mealtime. It may be interesting to note that I cannot remember to have ever “believed” in Santa Claus though we always celebrated Christmas with many presents and an excess of good things to eat. In the later teens, for interesting information about how various peoples have tried to set up their backgrounds for thought, I dipped now and then into the great religious books: The Koran, the Hindu books, the Bible, the Book of Mormon, the Meditations of Marcus Aurelius, Plato’s Dialogues and the like, all in English. After dozens and dozens of boys’ books had been read, including C. C. Coffin’s volumes on the American Revolution and the Civil War and stories like Little Lord Fauntleroy, Stockton’s Tinkham Brothers’ Tide Mill, Roe’s Driven back to Eden, Carrol’s Davy and the Goblin, I think my first serious venture in grown-up reading was Thoreau’s *Week* on the Concord and Merrimac Rivers. I must have read the latter when I was fourteen, the winter before I entered high school. In the next half decade I read much of Thoreau, Emer-

son, Carlyle, and so on. Thoreau’s writings may have influenced my development more than those of any other in those early days.

From the time I could handle hammer and saw I was forever “building things,” following more or less in the path of my father and older brothers. A treadle scroll saw was mine and was in almost daily use throughout four or five years before I entered the high school. In the high-school period I built two canvas canoes, but never used them because available water was too far away. In that period I built some glass-covered trays for our butterfly collection (my older brother Luther’s and mine) and made presses and cases for dried plants. Whenever mechanics could be observed at work I followed their every move. I am still greatly impressed by memories of the operations seen in a cooper shop and in a wooden-shoe shop passed on the way to school when I was about ten. I watched the neighboring blacksmith. A relative in a nearby village, whom I sometimes visited, was a cooper as well as a farmer. In early grade-school days I played games with other boys—such as leap-frog and pullaway—and made and flew kites in summer, built and used bobsleds, skated and caught rides on sleighs in winter. For a number of years I split and stored our firewood, kept the snow about our home shoveled in winter and ours and a neighbor’s lawn mowed in summer. I earned my first money by making toy furniture and by mowing that neighbor’s lawn. I still have a set of Shakespeare’s works bought with that lawn-mowing money—but the morocco-leather backs are now mostly gone.

Before I began to attend school I had seen flies’ wings and the like under a small compound microscope. It was in that same pre-school period that I brought some pieces of woody stems—such as those of raspberry—into our living room, at a season when the leaves were off, and cut thin sections of them

to examine under that little microscope. I think I was familiar with the appearance of cell structure and with tracheae of such small woody stems before I was eight years old. I was eight when I first went to school, where they started me in the third grade. Somewhat later my brother Luther had a larger microscope for a year or more, through which I was allowed to look now and then, but that instrument went away soon—it may have been borrowed—and my real beginnings in microscopy were in high-school days.

I suppose I must have learned a great deal in the grade schools, which I think were very good in that Michigan town at that time, but I am unable to recall many particulars of what was gained there. Orderly development of my conscious life seems to have begun with the high-school period, which was definitely formative for later things. It was of course in that period mainly that botany (Gray's *Lessons and Manual*), zoology, physics, algebra, geometry, chemistry, rhetoric, grammar, drawing and the like came really into my conscious field of mental vision. Following an English course throughout, I awoke to the need for other languages at the end of the second high-school year and I worked by myself at elementary Latin that summer and at elementary Greek the next summer, completing in school, as "extra work," the first three years of Latin and the first year of Greek. I never had any instruction in these languages beyond the reading of Cicero's orations and a little of Xenophon's *Anabasis*. Modern languages came later.

Almost from the very first I, more or less unconsciously, studied nature as well as books and people. Two older brothers were much interested in wild plants in a sort of quasi-scientific way, and I began to accompany one or the other of them on their Sunday trips to the woods as soon as they thought me old enough to go along. There were wild areas within easy walking distance of the terminals of

several street-car lines. I thus learned very early to name most of the conspicuous wild plants of that region and to know where one went to find each sort. We specialized a bit on native orchids. I remember buckets and pitchers of *Cypripedium spectabile*, *Habenaria psychodes*, *H. fimbriata*, *Calopogon*, and so on, which were arranged about the home on Sunday evenings after such trips.

In the high-school course in botany each student made an herbarium of one hundred or so plants. By that time I was botanizing on my own. I added to that herbarium for a number of years, till I went to Ann Arbor; and I received ten hours of advance credit in botany for my herbarium when I entered the University of Michigan. Without any arduous study I came to know many plants and their habitats, and the use of books like Gray's *Manual*, before I entered college. I never received any instruction in systematic or taxonomic botany anywhere excepting in the half-year course in high school.

After finishing high school I spent a week at the first Chicago World's Fair, a good deal of it in the horticultural building; then went to Short Hills, N. J., to work as laborer at Pitcher and Manda's great nurseries—at six dollars a week. My older brother Luther—a cataloger and bibliographer—had been making catalogs for that nursery and had spent a year in Colombia and Venezuela collecting *Cattleyas* and shipping them north. He and I lived together at Short Hills for a year, in a friend's barn, which we transformed into a passable cottage. We did our own cooking and were vegetarians. I worked in most of the various nursery departments, hardy perennials, palms and ferns, seeds and bulbs, orchids (there were several acres of orchid houses), packing room. I learned to do most of the things gardeners do; in the early autumn I got out the plants for orders for hardy perennials. The hardy grounds comprised about seven acres—just beds and beds and cold frames and

cold frames *ad lib*. Everything was labeled with the Latin name. My brother Luther was the first to use consistently Latin names and actual photographs for commercial florists' catalogs, at least in this country. There were many houses of ferns, palms, anthuriums, chrysanthemums—a great exhibition of chrysanthemums every fall. We were always interested in knowing the regions from which the plants had come. In my year there the firm was about the first to introduce Japanese iris in this country; we were propagating the first twenty varieties received from Japan. Traveling collectors sent in plants from various parts of the world and there were traveling salesmen who covered this country. One man did nothing but take photographs of plants. Foremen of the various departments and these traveling men became known later as heads of nurseries—Manda, Lager, Bobink and Atkins, *et al*. Their names are still familiar to gardeners. That firm, the United States Nurseries, did a great thing for garden and greenhouse botany and ornamental horticulture. They had a large exhibit at the World's Fair—some thirty enormous tree ferns among other things.

But that nursery never paid, and Mr. Pitcher had financial reverses about 1903–4 and ceased to pay the annual deficit. So they tried to curtail, and my year there was in the period of curtailment. I suppose there were thirty or more men employed in my time. After I left, to go to college, the firm went out of existence and their large and rare plants were sold at auction; the big tree ferns, which had come back from Chicago, were sold at five dollars each, for the roof of the old Madison Square Garden. In my time they were selling off the specimen plants and we were propagating cheap stuff, to try to "make some money"—greenhouse ferns in flats and 2–3-inch pots by the thousand, palm seedlings, etc. I remember working with one other chap for two or three weeks doing nothing but pot tiny fern plants from flats to

2-inch pots. There was a large field of *Lilium auratum* and *L. speciosum*, where, for several days, I cut tubs full of flowers—to go to New York and be auctioned for a cent or two a flower. With a Polish boy, I collected a thousand plants of Solomon's seal on the hill west of East Orange, to go to somebody's estate in England. One afternoon I collected one thousand stems of golden rod, for some girl's wedding in New York.

Saturday afternoons, Sundays and holidays, in this Short Hills period, I spent botanizing in the neighboring region—the hills around East Orange, the Newark marshes, etc. In early summer of 1894 I left the nursery and botanized every day till fall, when I went to Ann Arbor. The herbarium grew apace, but I never added to it considerably after that summer.

At the University of Michigan there was no one who cared especially for the taxonomic botany of higher plants, though Prof. V. M. Spalding was sympathetic with a plan I had proposed to catalog the plants of the Ann Arbor region according to habitat. We knew little or nothing of ecology, the word wasn't known to us, but Spalding knew natural vegetation very well. There was a fair local herbarium. I worked at this plan by myself for a year or two. In the meantime I "did courses" in plant morphology, physiology, animal embryology, chemistry, physics, German, French, Italian, and the "required" courses in mathematics, psychology, etc.—just one short and unsatisfactory course in English composition. I had studied Spanish with my brother at Short Hills—he had recently returned from South America and liked to speak that language. Because of my plan concerning plant distribution I asked Prof. F. C. Newcombe to let me take his lectures in plant physiology, omitting the laboratory work, but he said that would be only a half-year course and it would do me no harm to know a bit about physiological experimentation; furthermore, he would predict that after I had

completed that laboratory course I would find physiology more interesting than any other field of botany. How he reached that prediction I can't tell, but I became his laboratory assistant the next year and have stuck to physiology ever since. Newcombe was not interested in ecology, which was then just getting started under the leadership of Warming and Schimper. Their books were not available to me till I went to the University of Chicago in the summer of 1899. I was a confirmed enthusiast for physiology by then.

Luther became well known as a bibliographer and specialist in rare books. He was first with Dodd, Mead and Company and then—in partnership with one of the Messrs. Dodd—with Dodd and Livingston. The last named firm had a store on Fifth Avenue for several years at a later time, till Luther became librarian of the Widener Collection, which had been given to Harvard University after Harry Widener had been lost in the Titanic disaster. From a wheel-chair, Luther saw the famous Harry Widener Memorial Room in the great Harry Widener Memorial Library before the building was finished, but he died before he occupied it. At the present time the librarian in charge of that room is Luther's widow, who writes as Flora V. M. Livingston. My eldest brother, Lincoln, was a lawyer, first in Grand Rapids and then in Denver, but he died in middle age, after developing a law library in the last-named city.

The first summer vacation of my Ann Arbor period was spent in New York City, where my then widowed mother and I visited my brother Luther and a sister who was living with him, on 21st Street, near Ninth Avenue. Those months I devoted to a library study of plant geography. Prof. N. L. Britton gave me permission to study in the library room of the old botany building of Columbia University, on 49th Street, where I was to be found almost daily that summer, reading in many of the classic treatises on plant geography, De Candolle, Grisebach,

and others. At that time I first became acquainted with N. L. Britton and John K. Small, both of whom exerted a good deal of influence on my development. Columbia University soon moved to Morningside Heights. In that connection, I remember well a rainy Saturday afternoon in the summer of 1894, when Luther and I explored the woods and fields where the great university was going to make its home, as had recently been announced in the newspapers.

After leaving Ann Arbor, in June, 1898, I got me a job teaching an array of sciences (physics, chemistry, human physiology, physical geography, botany and zoology) in the high school at Freeport, Illinois. I found time to explore the neighboring country (with a bicycle), but did little with botany as such. I kept my alga growing in cultures in my bedroom window; the alga had been brought from Ann Arbor (discussed more fully below). In the late winter of 1898 I made applications for fellowships in about ten universities and received three appointments that spring—at Harvard University, University of Wisconsin, and University of Chicago. I became a fellow and assistant in the last-named institution, going there about the end of June. Prof. C. R. Barnes had been called from the University of Wisconsin the year before, to take charge of plant physiology and to edit the *BOTANICAL GAZETTE*. He gave very excellent lectures for elementary and advanced students; he prepared a set of laboratory outlines on the Detmer plan, which have become classic through his students, "grand-students," and "great grand-students." The conducting of the laboratory work was my own responsibility; on arrival, I was given the necessary keys and some outlines and was told that "the laboratory class would appear next Tuesday." Throughout the next four years, with some vacations, I conducted that laboratory, on the fourth floor of the Hull Botany Building near 57th Street, consulting Professor Barnes at times, but in all that period I think my

chief was never in the laboratory rooms more than perhaps twenty times. When he did appear he showed quite wonderful facility in handling experimental apparatus, but he always hurried away and he never interfered. He left the laboratory to his assistant but he always seemed to be aware of all that was going on there. On an early occasion, when I had asked him whether things were going forward as he wished, he replied, "You may rest assured that I will let you know if I think anything is going wrong." It was through his lectures and personal conversations that Barnes's students received guidance and inspiration from him, and through the sometimes peppery reviews that he prepared for the *BOTANICAL GAZETTE*. I think Barnes's mental processes and his facility in presenting his thoughts were more nearly perfect in precision, clearness and completeness than those of any other person with whom I have ever worked. I was indeed fortunate to be his first active assistant at Chicago. His publications in plant physiology were few, but his mind and personality exerted a profound and lasting influence on the development of this science.

At that time Goodale held a professorship in plant physiology at Harvard University, but Newcombe, MacDougal and Barnes were, I think, the first with that title to devote themselves primarily to physiology in this country. In these early years of the present century, plant physiology was in the incunabula or even embryonic stage of its development here, although it had already become a distinct science in Germany, especially at the hands of men like de Vries, Sachs, Detmer, and Pfeffer. Newcombe had been inspired by Pfeffer and it seemed to give the fine old Geheimrat some pleasure when, in 1908, in his Leipzig laboratory, I remarked to him that I was his "intellectual grandchild." The three volumes of Ewart's classic English translation of Pfeffer's *Pflanzenphysiologie* appeared in the very earliest years of this century.

In those times American botany had, in most places, already relegated plant taxonomy to the basement, and its main quarters were occupied by Strasburger morphology and the beginnings of cytology; physiology was still generally struggling in attic rooms, and ecology—a sort of regenerating outgrowth of taxonomy, floristics and plant geography—was just beginning to be considered. It was notable that three professors of plant physiology were appointed about 1909, at Washington University (St. Louis), at Harvard University and at The Johns Hopkins University. A number of assistant professorships and instructorships in the new science were already in existence in this country and interest was turning in that direction.

Throughout my Chicago period I was greatly attracted toward the field of ecology, which was being rapidly developed there under the general leadership of Professor J. M. Coulter and at the hands of the young H. C. Cowles. Like Asa Gray, Coulter had realized the possibilities of the newer phases of botanical study that were attracting so much attention in Germany. A taxonomist himself, he encouraged Chamberlain and Cowles—who were among his earliest Chicago students—to devote themselves respectively to the morphology, histology and cytology of reproduction and to ecology. Cowles was coming into ecology from geology and plant taxonomy (see *ECOLOGY* for July, 1935) and his main interests lay in the details of local plant distribution. That was exactly the field towards which I had been groping, with the encouragement of Spalding, in the early part of my Ann Arbor period and it inevitably appealed strongly to me when I became intimate with Cowles at the time of his classic sand-dune studies. Cowles's great contribution was toward what he called physiographic ecology, which dealt with local features of distribution in terms of the physiographic characteristics of the corresponding plant habitats; he and his students studied vegetation rather than

plant individuals or species, in bogs and swamps, on beaches, flood plains and bluffs, on moraines, in ravines. Glacial topography was just as important in this as was plant taxonomy, and the concepts of plant physiology always entered into these studies to a considerable degree. For that period I add the name of Cowles to those of Newcombe and Barnes as representing the personal contacts that most influenced my own scientific development.

In my last year at Ann Arbor I had carried out a somewhat elaborate experimental physiological study on the influence of the osmotic characteristics of liquid culture media on the growth and development of a small polymorphic freshwater alga, and that study was continued throughout my Chicago period. (See "The rôle of diffusion and osmotic pressure," Chicago, 1903.) That was also, of course, an experimental study in the ecology of that alga, and it turned out that the polymorphism of the latter might be controlled—as we used to say—not only by the osmotic characteristics of its environment but also by environmental characteristics that influence water absorption and water loss; a relatively strong solution of non-toxic solutes acted on the cells as a drying agent and similar effects might be produced by exposure to the air (evaporation).

It was thus natural and easy to try to find for ordinary plants relations of vegetational differences to the drying influences and water-supplying influences of air and soil. I had the thought that the physiographic conditions emphasized by Cowles might be effective largely in that way. For the pine plains of Michigan, which I studied in the summer of 1901 (see *BOTANICAL GAZETTE*, 1905), it turned out that upland vegetation types were rather nicely correlated to the water-holding capacity (size of particles) of the surface soil, which appeared to determine water supply and soil aeration, for the macro-climate is essentially the same for the whole of the region considered. This seemed to mean that upland vegetation

differences in those plains might be mainly due to differences in soil-moisture content in summer; sandy uplands were generally dry unless the soil was much modified by humus, and clayey uplands were generally moist, the more so as the humus content or covering of the soil was greater. Lowlands were generally moist or wet whether the mineral constituents of the soil were sandy or clayey—because there the subterranean water table was at the soil surface or not far beneath it.

That bog water might perhaps differ from the water of drained swamps by having a much higher osmotic value had been deduced from Schimper's brilliant but cryptic observation that bogs are "physiologically dry." That deduction was easily shown to be untrue—by cryoscopic tests carried out on samples of water from various bogs and swamps of Michigan and New Jersey. These waters were then tested by employing my alga as an indicator and it emerged that water from about the roots of typically bog plants acted on the alga as if it contained stimulating or slightly toxic solutes. Bog waters were generally more acid than the others (by titration tests; H-ion concentration and the now familiar pH did not appear on the physiological and ecological stage till somewhat later), but their stimulating or toxic influence was apparently not directly related to total acidity. Perhaps I was dealing to some extent with some cryptotrophic or cryptotoxic solutes in bog water, presumably of organic nature, and my accounts of these studies now seem to suggest substances more or less resembling some of the hormone-like substances now being studied so vigorously in both animal and plant physiology.

While at the University of Chicago I listened to several series of lectures on plant morphology given by Coulter, an inspiring teacher whose talks and writings are fine examples of excellent presentation. What I remember of Coulter centers about his fine personality and his remarkable facility of expression. Of course his fundamental philosophy or out-

look on things in general was not physiological. He always tried to avoid the implications of teleology but one felt that he was perhaps only half-hearted in that. Barnes's attitude towards the problems of causation—in plant activity, development and evolution, and apparently in everything—was similar to that shown in Pfeffer's later writings and in those of Loeb; light on problems of determination and causation was to be sought in terms of the properties or characteristics of matter and energy, and teleology and anthropomorphism were to be avoided wherever the nature of language would permit. I was afterwards much impressed and encouraged in my attempts at clear thinking and writing by Verworn's little essay on *Kausale und Konditionale Weltanschauung*, but encouragement came to me mainly in those years from Barnes and Loeb.

Loeb's general course in physiology broadened my field of intellectual and philosophical vision very greatly. My *Weltanschauung* seems always to have been of the etiological rather than of the teleological sort, but most writers whom I read continually indulged in teleology or even in out-and-out mysticism. Over-enthusiastic as he often was, Loeb's characteristic approach to physiology from the standpoint of physical and chemical concepts represented a remarkable forward step in the fundamental biological thought of that time. It soon became a sort of vogue to point out where his interpretations and generalizations were far too simple to find full support in the results of subsequent experimentation, but what we call his mistakes of over-enthusiasm turned out to be valuable contributions; where he went too far he led others to proceed more slowly in the same direction. I think I perhaps received somewhat more edification from Loeb than from Barnes, but both men exerted enormous influence in my formative period. There were times when I decided that animal physiology should be my field, but Loeb always advised against a change.

Although he was always enthusiastically sympathetic with my problems and findings, he did not offer me a fellowship in his laboratory, and so I remained in the plant physiological field.

From chemical studies of a quasi-research nature under the guidance of Gomberg (at the University of Michigan) and of Lengfeld and Stieglitz (at the University of Chicago) I gained much in appreciation of the physical and chemical bases of vital phenomena. As is generally true for any group of young men studying in a university—or elsewhere, for that matter—the graduate students and instructors at the University of Chicago exerted great influence on the mental development of one another. I gained much from intimate friendship with men like H. N. Whitford, W. B. McCallum, H. Hasselbring, J. B. Overton, O. W. Caldwell, J. P. Goode, A. W. Greeley, and the rest.

My native instincts were perhaps as much bent toward literary art as toward the intellectual field of science. Language and its use have always claimed much of my attention by the way but, aside from elementary high-school and college courses in Latin, Greek, German, French, Italian and English, my education in this general field was informal and self-conducted. I have always been wont to devote a good deal of time each week to general reading of eminent and less eminent writers. Never becoming expert with any foreign language, I dabbled superficially in many, being able to read easily only German and French, however. It has always been pleasant to study the dictionary, especially for etymologies and the finer shades of word meaning.

A part of one summer of my Chicago period was devoted to teaching botany in the Eastern Illinois State Normal School, at Charleston, where I had many very pleasant and inspiring conversations with the president of that school, L. E. Lord.

Toward the end of my Chicago period I spent an autumn at the New York

Botanical Garden, in an experimental study of the influence of a number of inorganic salts on the polymorphic green alga mentioned above. It was at that time that I became acquainted with MacDougal, Lloyd, H. M. Richards and C. C. Curtis, all of whom were very helpful and encouraging. The following summer, and a grant from the Carnegie Institution, were spent in study at the new Desert Laboratory, with Cannon and Lloyd. From the study of desert plants came many new ideas, especially with respect to water supply and water loss. My interest in osmotic pressure and soil dryness as environmental features was broadened to include evaporativity and the drying influence of sunshine. The porous-porcelain atmometer was devised and first used by me at that time—but I afterwards learned that it had been independently devised at least twice before, by Babinet and by Mitscherlich. After the experiences of that first summer at Tucson transpiration and water supply were among the topics that I found most interesting. They enticed in many directions.

Returning from Tucson in September, I spent the following autumn at the U. S. Bureau of Soils, in Washington, where I gained much from conversations with Whitney, Cameron, Schreiner and a number of other members of the bureau staff. We were studying the possibility that some soils might contain chemicals that acted to retard plant growth therein. I returned to Chicago for the winter quarter at the University and then received my first appointment to a permanent position, in the Bureau of Soils. That position was not very permanent, however, for I resigned and entered the staff of the Desert Laboratory the following January. MacDougal was the newly named director of that laboratory and my studies in physiological ecology—especially on relations of plants to soil moisture and to evaporation—were continued with his encouragement. I remained at Tucson till

the next December, spent that winter and the early spring in eastern institutions, partly in library studies but mostly in experimentation at the Missouri Botanical Garden, at St. Louis, where I gained much from pleasant contacts with William Trelease, H. von Schrenck and J. A. Harris. That St. Louis period was devoted to a study of transpiration in greenhouse-grown cacti. The year 1908 was spent in Europe, mainly at Munich, where I learned a great deal from von Goebel's lectures and field trips and from Hegi's botanical-geological excursions. Renner, who was studying the physics of plant transpiration at that time, was my frequent companion and I owe much to his keen mind. At Munich I was engaged in studies on soil moisture and it was there that I first devised and tested the porous-porcelain soil-moisture "meter," which has recently been independently developed by Rogers and others. In the autumn I spent a few weeks at Pfeffer's institute at Leipzig and had the good fortune to have some conversation with the Geheimrat almost daily. I also visited and became well acquainted with Klebs and Glück, at Heidelberg, and made tourist excursions through Germany and Switzerland. In the early winter I spent a few days at the Rothamsted Station in England, where Hall was then director. At the end of 1908 I attended the Baltimore meeting of the American Association and associated societies on my way back to Tucson. It was at the time of that meeting that I first saw the late Professor D. S. Johnson's recently established garden, on the newly acquired Homewood tract which was to become the home of The Johns Hopkins University. At the close of that meeting Johnson led a day's excursion through the snowy woods and fields north of Cockeysville, Maryland, in which Lloyd and I took part. That was a memorable occasion; we were almost cold and became more than almost hungry, but were withal exceedingly enthusiastic

over many different sorts of botanical observation and discussion.

Another memorable excursion from which I gained a great deal was from Tucson to the Salton Sea, in the early summer of 1909. It was arranged by MacDougal partly for several visitors. We spent a day or two around Yuma, a day at Yuma Junction and a week in camp near the U. S. Weather Bureau's evaporation station, where we became acquainted with the field studies, in evaporation, of Bigelow and his associates, who were very busy there with pans and tanks, anemometers, thermometers, and psychrometers. We operated atmometers, examined the neighboring desert hills and the newly-formed beach, visited Pelican Island and the place on the shore from which pumice fragments, worn to rounded pebbles and boulders, were floating away. I afterwards referred to those floating stones as notable examples of a remarkably perfect "adaptation" in the realm of the non-living.

While on that trip I received a forwarded telegram asking if I would consider an appointment as professor of plant physiology at The Johns Hopkins University, and my affirmative reply was sent, on a Sunday evening, from the railway office at Yuma Junction (where the branch for El Central leaves the main railway line), while the west-bound train halted for a quarter-hour; the appointment was authorized in Baltimore on the following day.

In the early fall of 1909 I attended the Winnipeg meeting of the British Association, after which Blakeslee and I made a short trip by boat, north from Kenora, on the Lake of the Woods, and I then became a resident of Baltimore. At the Winnipeg meeting I became well acquainted with Yapp, who had been studying evaporation influence on a spiraea and other plants, also with Gwinne-Vaughan, Wager and others from abroad.

The first year at The Johns Hopkins University I lectured in the old Biology

Building on Eutaw Street (the place is now a parking lot) and conducted a laboratory course and research in the small building and greenhouse which already stood on the Homewood grounds, at the south side of the new botanical garden. Among those who studied with me that first year were F. H. Blodgett, L. A. Hawkins, W. D. Hoyt, W. R. Jones, L. W. Sharp, H. H. York and W. H. Brown. Brown³ is about to come from Manila to be lecturer in botany here. Our group was an ideal one, working in an ideal atmosphere, and I gained as much from those students as they gained from me.

With the help of Hawkins and others, I soon devised and constructed the first rotating table for use in the standardization of atmometers. That table, which is eight feet in diameter, first stood in the attic of the small building just mentioned; it is now on the upper floor of the Laboratory of Plant Physiology (fig. 2), where it is still occasionally used. Two or three years later Shive and I introduced rotating tables for series of simultaneous plant cultures, and such tables for equalizing aerial conditions in experiments with plants soon came into general use in many laboratories. After Sam F. Trelease and I had introduced the employment of continuously flowing solutions in solution-culture experimentation it became desirable to arrange for continuous flow in cultures on rotating tables, but that was not actually accomplished until 1934, at the hands of Ch. Zinzadze and Karl A. Grossenbacher.

The present laboratory was completed in the early winter of 1911-1912. My personal study throughout much of the preceding year had been devoted to the interior details of this building; all cases, tables, sinks, the electric wiring, and so on, had been specially designed, to produce a small, compact and very efficient working unit. In a great many of the

³ Brown died at the end of that academic year.

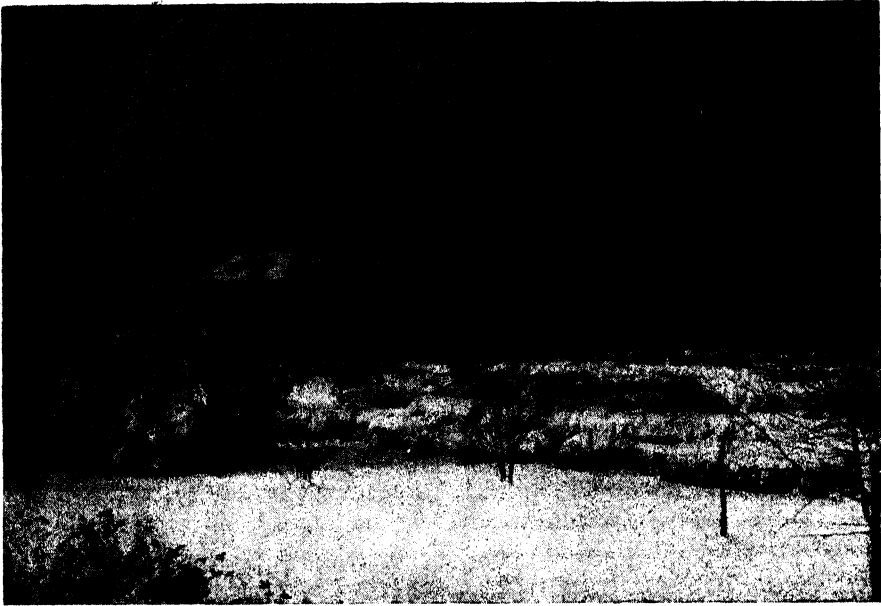


FIG. 2. The Johns Hopkins University Laboratory of Plant Physiology at Homewood, Baltimore, Maryland.

arrangements I was aided by students, most of whom were good mechanics. The laboratory has served its purpose excellently for a quarter of a century.

For several years after coming to this University I returned to the Desert Laboratory each summer for a period of three or four months, continuing along lines of study that had been opened in my Tucson period. Each of these summers I had, through small grants of funds from the Carnegie Institution of Washington, the help of one or more assistants—young men who were about to receive, or had just received, their Ph.D. degrees, either here or elsewhere. Following is a list of these men, to all of whom I owe a great deal: W. H. Brown, J. S. Caldwell, E. M. Harvey, H. E. Pulling, J. W. Shive, A. L. Bakke, H. C. Sampson, E. S. Johnston, J. D. Wilson, L. J. Pessin, M. Fraps.

The summer of 1915 was spent in the region between The Pas and Split Lake, Manitoba, on a canoe trip, in company with H. E. Pulling. The new Hudson Bay railroad was partly constructed—as

far as the bridge, at Manitou Rapids, on the Nelson River—and we had the benefit of transportation aid from the men in charge of construction and fire inspection. Without any guide, we traveled slowly on lakes and rivers from Picotinay to Split Lake Post and then ascended the Nelson past Grand Rapids to Manitou Rapids, whence we returned by railway. On that trip we gained an excellent general knowledge of the vegetational conditions of that general region.

After the new railway had been completed to Churchill, Mrs. Livingston and I visited that place, in the summer of 1935, where we lived for a week in a room in Mrs. Riddock's woodshed and explored the nearby region, with help from the officials of the new grain port. Although I had for years a desire to visit the country beyond the northern limit of forest, I never really passed beyond that limit, which is apparently not far north of Churchill. My "farthest north" is the old Hudson Bay Post at Fort Churchill, across the river from the new town of Churchill. I was much impressed by

seeing a large plant of the small white lady's-slipper in full bloom (about July 6, 1935) at the side of the age-old trail on the north side of the Churchill River; we also were interested in the gardens of residents of The Pas, where, in early July, we saw the yellow cypripedium and *Cypripedium spectabile* in full bloom, also the most vigorous plants of the perennial delphinium I have ever seen anywhere.

On that second trip to the North we motored from Baltimore to Winnipeg, attending the Minneapolis meeting of the science societies on our way, and, returning from The Pas, we motored from Winnipeg to Duluth, took a lake steamer to Sault Ste. Marie and then motored back to Baltimore from that point, stopping at Mackinac Island and other places.

With Mrs. Livingston I spent the summer of 1921 at the Desert Laboratory, continuing earlier studies with Forrest Shreve. The book on climates and vegetational types of the United States, which had occupied Shreve and me for a period of ten years, was published in that year.

The summers of 1922 and 1926 were spent at the Desert Laboratory, but I have not been there since.

To complete this survey I add below a list of those who have received the Doctor's degree with me at The Johns Hopkins University.

DOCTORS OF PHILOSOPHY IN PLANT PHYSIOLOGY FROM THE JOHNS HOPKINS UNIVERSITY, 1909-1939

(Date of degree in parentheses)

| | |
|------------------------|--------|
| Coggeshall, Mary | (1931) |
| Darrow, G. M. | (1927) |
| Edwards, T. I. | (1932) |
| Espino, R. B. | (1919) |
| Fawcett, H. S. | (1918) |
| Free, E. E. | (1917) |
| Gericke, W. F. | (1922) |
| Haasis, F. W. | (1928) |
| Hawkins, L. A. | (1913) |
| Hildebrandt, F. M. | (1917) |
| Hutchins, L. M. | (1924) |
| Johnson, E. S. | (1917) |
| Lawrence, D. B. | (1936) |
| LeCompte, S. B., Jr. | (1939) |
| Mack, W. B. | (1929) |
| Marshall, Robert | (1930) |
| Matz, Julius | (1932) |
| McCall, A. G. | (1916) |
| McLean, F. T. | (1915) |
| Norem, W. L. | (1936) |
| Pardo, J. H. | (1932) |
| Shive, J. W. | (1915) |
| Swingle, Charles F. | (1927) |
| Tang, Pei-Sung | (1930) |
| Tottingham, William E. | (1917) |
| Trelease, S. F. | (1917) |
| Veerhoff, O. L. | (1937) |
| Veihmeyer, F. J. | (1927) |
| Verner, Leif | (1934) |
| Wilson, J. D. | (1926) |

ECOLOGY OF DESERT PLANTS. I. OBSERVATIONS ON GERMINATION IN THE JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA

F. W. WENT

*Kerckhoff Laboratories of Biology, California Institute of Technology,
Pasadena 4, California*

INTRODUCTION

Plant communities exist due to interaction between the individual members and between these and the environment. This introduces such a complexity, that a physiological analysis of the community as a whole seems impossible at present. But as the starting point of such an analysis the desert communities offer an unusually favorable opportunity. In the first place the vegetation cover is not closed, so that interactions between plants are greatly reduced, and their influence on each others' immediate surroundings is relatively small. Under such conditions direct correlations between plants (the influence of one plant on the other) are more easily found, as shown by Went ('42). This wide spacing of the plants is of special importance in germination, because that process tends to occur much more frequently in open areas than in a closed cover of existing vegetation.

In still another respect, desert plants are particularly favorable experimental material. They are subjected to more extreme conditions than other plants, so that their responses can be expected to be geared to greater climatic differences. Therefore laboratory experiments are likely to show larger differences in response than when plants of more equitable climates are used.

Finally, everything which happens in the desert vegetation can be rather easily attributed to distinct climatic occurrences such as a particular rain.

With these considerations in mind a series of trips were made, during the years 1945-1947, to study the vegetation of the Joshua Tree National Monu-

ment, located 200 km. (130 miles) due east of Los Angeles. The altitude of the areas most commonly visited varies between 800 and 1500 m. (2500-5000 ft.).

The San Bernardino and San Jacinto mountains shield the area from the climatic influence of the ocean. Along its west boundary the Little San Bernardino Mountains, reaching a height of 1700 m., separate the area from the Coachella Valley. From the west the altitude of the broad valleys of the National Monument falls gradually to 800 m. in the north and east, with intervening mountain ranges.

The climate can best be described with the help of figures 1, 2 and 3. Climatic records are kept by the Cooperative Weather Station at Twentynine Palms, just north of the Monument at 650 m., and daily temperatures are recorded at Hidden Valley at 1400 m. by Mr. Randolph.¹

Annual rainfall at Twentynine Palms amounts to 136 mm. but at Hidden Valley and higher altitudes in general the rainfall is considerably greater, especially during July, August and September, when thunderstorms break over the mountains. Figure 1 shows the monthly distribution of rainfall, the number of cloudy days and the relative humidity in the afternoon at Twentynine Palms, with an indication of the seasonal differences in rainfall. The winter rains are fairly evenly distributed over the whole National Monument, but the summer rains are highly localized, as figure 2 shows. This figure gives the approximate location of rainbursts ac-

¹ The assistance given by both the Rangers of the Joshua Tree National Monument and Mr. Randolph in making these and other data available is gratefully acknowledged.

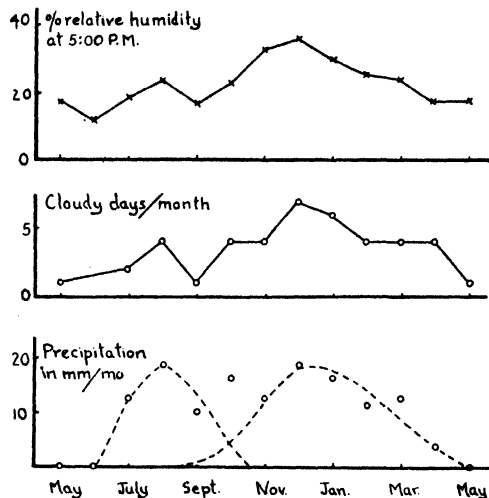


FIG. 1. Meteorological observations at Twentynine Palms (altitude 650 m., eleven year average). Top curve: mean relative humidity of the air at 5:00 P.M. Middle curve: mean number of cloudy days per month. Lower curve: mean monthly precipitation in mm. There are obviously two peaks, one in August and one in December, corresponding with the summer thunderstorms and the winter rains.

companying thunderstorms during the summer of 1946 in the Monument, as observed by Rangers and Fire Guard, and as evidenced by washouts in roads.

Figure 3 shows the weekly mean minimal and maximal temperature at Twentynine Palms and Hidden Valley throughout the period of observation. There is approximately 6° C. difference in minimal and 7° C. in maximal temperatures between these two localities, which differ 750 m. in altitude.

Below 1200 m. the dominant shrub is *Larrea divaricata* Cav. (see fig. 5); around 1500 m. *Pinus monophylla* Torr. et Frem. and *Juniperus* characterize the plant cover of the rocky slopes; and between 1000 and 1500 m. the Joshua-tree (*Yucca brevifolia* Engelm.) typifies the landscape with its branches reaching weirdly heavenwards (see fig. 4). There is a rich growth of low desert shrubs at all altitudes so that botanically speaking this area should be called a desert scrub region rather than a desert.

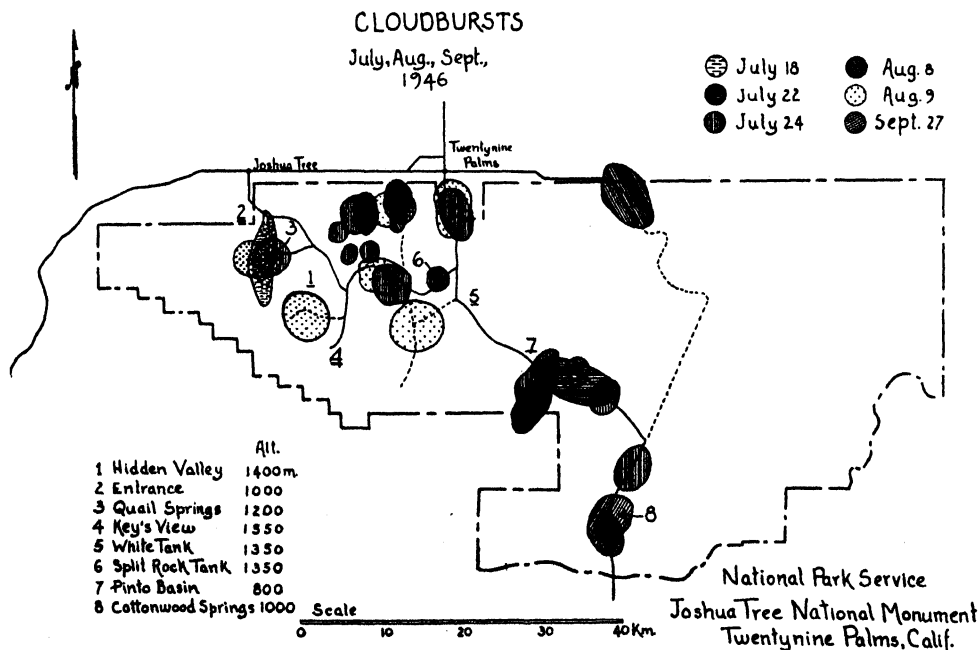


FIG. 2. Occurrence of thunderstorms in the summer of 1946, within the boundaries of the Joshua Tree National Monument. Since observations were only made along the roads, thunderstorms in outlying places (such as the Eastern part of the Monument) are not recorded. For the commonly visited regions all thunderstorms are recorded.

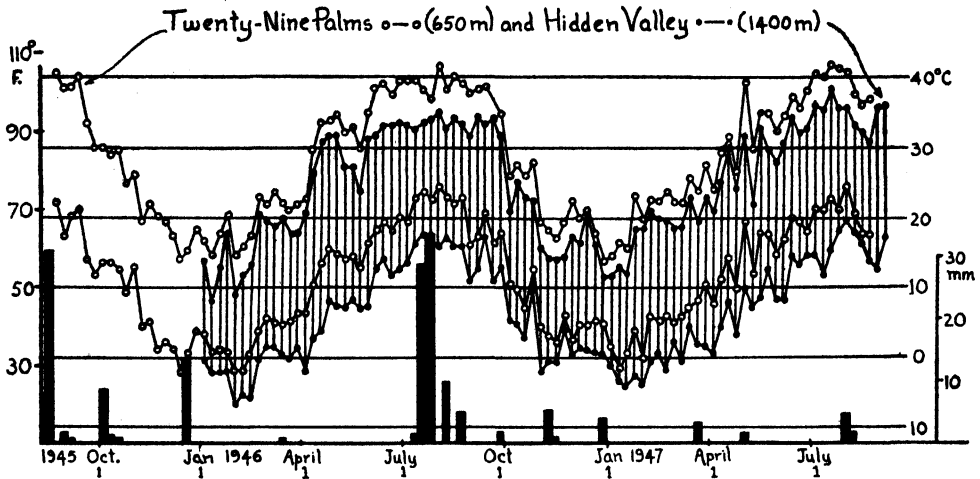


FIG. 3. Weekly average maximum and minimum temperatures at Twentynine Palms (open circles) and at Hidden Valley (dots). Temperature range at Hidden Valley represented by vertical lines. Black columns indicate weekly total rainfall in mm. In both winters rainfall has been exceptionally low.

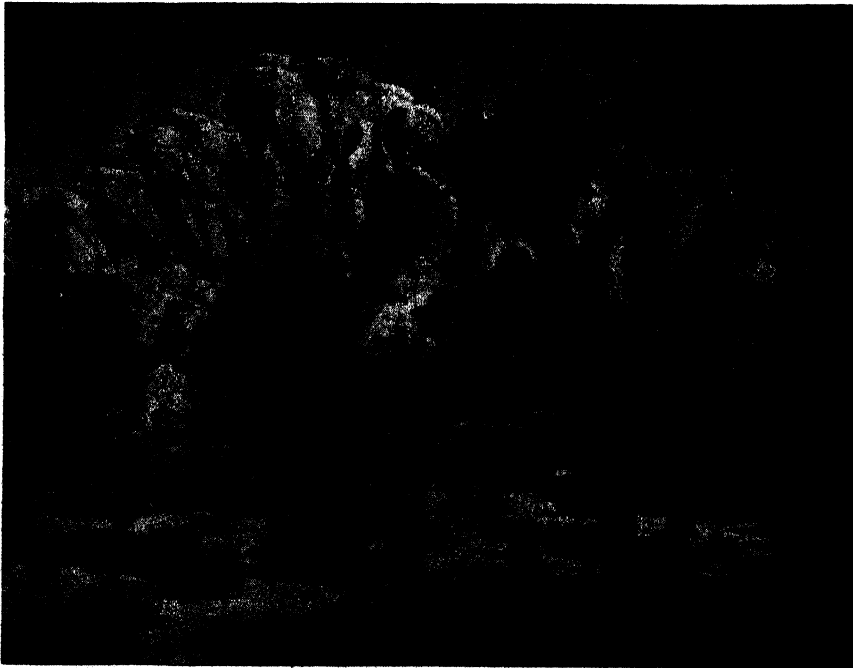


FIG. 4. Hidden Valley in Joshua Tree National Monument. In right foreground *Yucca brevifolia* (Joshua Tree), in center background against rocks *Quercus dumosa turbinella*, left background *Pinus monophylla*. The small shrubs on desert floor are mainly *Hymenoclea Salsola*, *Coleogyne ramosissima*, *Hilaria rigida*, *Salazaria mexicana* and others. Photograph by S. Wildman.

Some additional observations were made at lower altitudes, to 80 m. below sea level, in the Colorado desert and in Death Valley, regions where much higher temperatures and lower precipitation prevail. The observations in Death Valley are reported separately (Went and Westergaard, '48).

FIELD OBSERVATIONS

The following description is based on field observations in May 1945, and approximately monthly visits of one or more days from August 1945 on to the end of 1947. The maximum and minimum temperatures during that period are shown in figure 3.

Observations were made on the germination, noting number of seedlings and as far as possible the species germinating. For this purpose seedlings were brought back to the laboratory and grown in the greenhouse to maturity, or to the stage where they could be definitely recognized. The observations will be recorded according to the germination and growing habits of the plant.

First the summer annuals will be discussed. These plants are found exclusively after summer rains, and have the shortest life cycle of any of the plants found in the desert. This is mainly due to the high temperatures at which they grow.

The second group consists of spring annuals which germinate exclusively in winter and flower in spring. This group consists largely of the smallest annuals found in the desert; many of them have rosettes and are long-day plants. Their development in nature is rather slow because of the low winter temperatures.

The third group consists of the summer and fall-germinating spring annuals. The plants of this group are large, and are not so restricted in their season; sometimes they are found to flower in autumn or in the middle of winter, when they have had a sufficiently long growing period in fall due to frequent summer and autumn rains.

The plants of the fourth group are not restricted in their time of germination, but they grow at almost any time when



FIG. 5. Summer aspect of desert at White Tank, after summer rains (Photo September 3, 1945). Shrubs: *Larrea divaricata*; sand covered with *Pectis papposa*.

the temperatures are not too low and with sufficient moisture.

As a fifth group all shrubs will be discussed together since they respond rather uniformly to climate, during the seedling stage.

A sixth group, perennial herbs, is so poorly represented in the area that it does not need special discussion (e.g., *Hilaria rigida* (Thurb.) Benth. which never was found germinating).

Summer annuals

1. *Amaranthus fimbriatus* (Torr.) Benth. was found in the Joshua Tree National Monument in the Pinto Basin (September 2, 1945 and September 7, 1947) and the Hidden Valley area (September 2, September 22, October 13, 1945; August 17, 1946 and September 7, 1947) and surroundings. After regularly spaced rains it grows to a height of more than 1 m.; otherwise the plants may be only 10 cm. high. It usually grows among shrubs.

2. Some introduced *Amaranthus* species such as *A. retroflexus* L. and *A. deflexus* were found occasionally after summer rains, but not at all during winter (Hidden Valley, Willow Hole, etc., in September 1945, August 1946, and September 1947).

3. *Aristida adscensionis* L., an annual summer grass, was found only at low altitudes in the Borego and Imperial Valleys.

4. *Boerhaavia spicata* Choisy var. *Torreyana* Wats. has the same distribution as *Amaranthus fimbriatus*. At lower altitudes (Borego Valley, Salton Sea) *B. intermedia* Jones is found. At intermediate altitudes (Pinto Basin, Cottonwood Springs) both *Boerhaavia* species grow side by side and flower at the same time (September 7, 1947); both are found only after summer rains.

5. *Bouteloua barbata* Lag. and *B. aristidoides* (H.B.K.) Griseb. Both of these are annuals, whereas most of the other *Bouteloua* species are perennial. Their distribution practically coincides with that

of *Pectis* (see No. 8 below). They only germinate after summer rains, and form ripe seed within 4 weeks at altitudes below 1000 m., and in 6 weeks at higher altitudes. If towards the end of their life-cycle new rains occur they usually sprout again from their root-crown but no new germination occurs after such autumn rains. If resprouting happens when the temperatures are much lower than is usual in summer, the new shoots remain exceptionally short and each inflorescence may consist of only a single spikelet. This was observed on November 25 and December 16, 1945 in the Hidden Valley areas, especially with *Bouteloua barbata*.

There is a slight difference between *B. barbata* and *B. aristidoides* in their vertical distribution. In the Hidden Valley area and other locations over 1000 m. altitude *B. barbata* is the more abundant, with fewer specimens of the other. In the Pinto Basin *B. aristidoides* outnumber the other species perhaps 100:1, and at other low elevations (Borego Valley at 300 m., Desert Center at 400 m.) *Bouteloua aristidoides* predominates.

6. *Euphorbia setiloba* Engelm. and *E. micromera* Boiss. These are annuals among the Euphorbias, and these too only germinate after summer rains. This is also the time that *Euphorbia polycarpa* Benth. germinates and resprouts from its perennial rootcrown. Their distribution is about as wide as that of *Pectis*.

7. *Mollugo Cerviana* (L.) Ser. Is locally very abundant after summer rains only. Was found growing in the Hidden Valley area on the same dates as *Amaranthus fimbriatus*; in addition large dry stands were found in Borego Valley on November 10, 1945. On September 7, 1947, it was abundant throughout the Joshua Tree National Monument.

8. *Pectis papposa* Gray (figs. 5 and 6). The yellow flowerheads of this fragrant annual composite produce a spectacular display in the desert after extensive summer rains, as on September 1-2, 1945, in Pinto Basin and along the northern

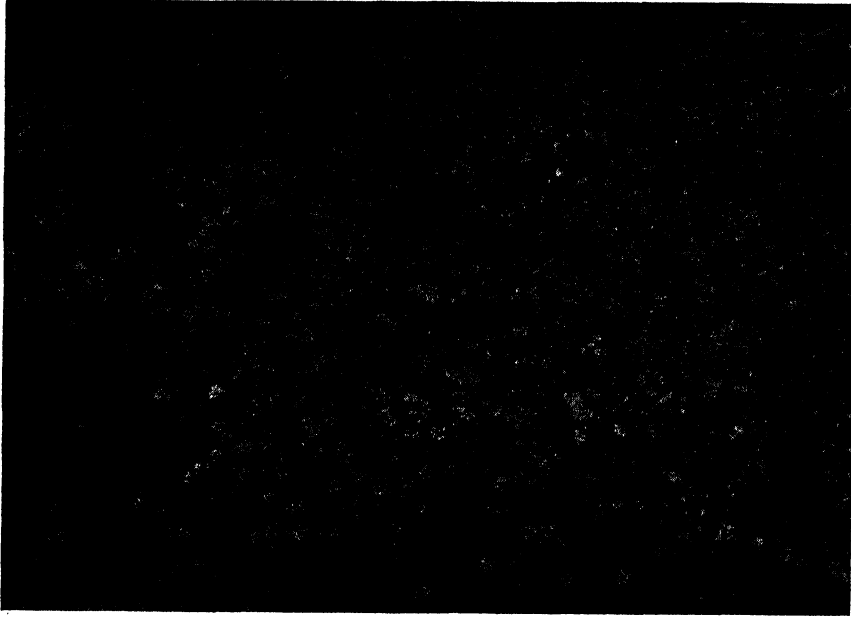


FIG. 6. Close-up of *Pectis papposa* near Split Rock Tank (August 17, 1946). Left foreground: *Sphaeralcea ambigua*; center: *Amaranthus fimbriatus*.

edge of the Joshua Tree National Monument, with a density of 100–1000 plants/m². Most of the plants were large (about 15 cm. tall) due to weekly rains which began on August 1 that year. In Hidden Valley area only scattered plants were found. On September 22–23 most *Pectis* plants in the Joshua Tree National Monument were in seed, and almost none were still in flower. This means that no further germination occurred after that of early August, and that later in the season none of the more recently produced seeds germinated.

On October 13, there were none growing except at Twentynine Palms, where a few small plants flowered. Later, on trips of November 25, December 16, January 6, 1946 and January 20, February 27 and June 17 not a single living *Pectis* was observed anywhere in the National Monument or the areas just north of it. On August 17, 1946, there were a few very small *Pectis* plants in the Hidden Valley area, but farther east where some good rains had occurred in July (see fig.

2), *Pectis* was locally very dense and well developed (e.g., near Split Rock Tank, fig. 6). On October 12 nothing was left of the *Pectis* and this plant was not found anywhere in the National Monument on November 25, December 23, January 19, 1947; February 8, May 4. On August 18, 1947, an abundance of seedlings was found in the southern part of the Monument, near Cottonwood Springs, where heavy rains occurred on August 7. In the Pinto Basin and Hidden Valley no *Pectis* seedlings were found, because the first heavy rain occurred there on August 16 and 17. It was flowering there on September 6.

In the lower deserts *Pectis* was found in 1945 at a later date than in the Joshua Tree area. On November 10–12 it was still fairly abundant around the Salton Sea at about sea-level (Travertine Rock, Borego Valley) but in early spring 1947, and in earlier years (1941, 1942) during spring, not a single *Pectis* was found there. On October 20, 1945 *Pectis* was also found near Baker in the Death Valley area, at

about 300 m. altitude. In May 1947 it was found flowering in the Palm Springs area at about 100 m. altitude.

Pectis has an exceptionally great range altitudinally: from minus 80 to plus 1400 m., and over all of this range except the lowest part, it can be stated categorically that *Pectis* only grows after the summer rains. At the lowest altitudes it is found also after autumn or spring rains, but in no part of its range has it been found after the winter rains, even as seedlings. Observations indicate that the amount of rain in a given shower as well as the season is important; a rain of slightly over 10 mm. at Split Rock Tank on August 7, 1947 did not cause any germination of *Pectis*, whereas rains of over 25 mm. are completely effective.

9. *Portulaca oleracea* L. Has been introduced and grows near camping places at Hidden Valley and Quail Springs. It was found in August–September 1945, August 1946 and September 1947, and recent germinations were found on November 25, 1945, apparently after an October rain which did not cause germination of any of the other summer annuals.

Winter germinating spring annuals

The majority of annuals belong to this group. No complete list of them will be given, and only a few plants will be discussed in more detail. Most of the smaller species germinate only in winter and are not even found as seedlings after autumn rains.

Both the 1945–1946 and 1946–1947 winter seasons were relatively dry in the Joshua Tree National Monument. The rains which did occur were mostly in the middle of winter when temperatures were too low for germination. When temperatures became more favorable the surface layers had become dry again.

1. *Boraginaceae*. Many members of this family are winter annuals. No seedlings of any *Boraginaceae* with the exception of *Amsinckia* were observed during summer, but they were found near Hidden Valley on December 16, 1945,

January 6 and November 25, 1946. Also in all other areas *Cryptantha* and *Pectocarya* were observed to germinate only in winter. On September 6, 1947 two *Cryptantha* seedlings were found in Hidden Valley against the northeast side of a large rock. Since the night temperature had dropped nightly to 10°–13° C. for a period of 10 days after the rain of August 16–17, this indicates that under those conditions this rain had taken on the character of an autumn rain.

2. *Descurania*, *Platystemon*, and others were only found as seedlings in December and January.

3. *Eriophyllum Wallacei* Gray. This plant germinates almost exclusively after winter rains. No seedlings of it were found in August–September 1945, August 1946 or August–September 1947, after extensive rains. Apparently a very few seedlings germinated in October 1945, since three minute flowering *Eriophyllum* were found on November 25 and two on December 16, 1945, in Hidden Valley. They were on the north side of rocks where apparently it had been somewhat cooler, but these few plants showed that it was an exception instead of the rule.

After wet winters it is very abundant around Hidden Valley; on February 27, 1946 and January 19, 1947, many seedlings of this species were found there.

4. *Filago*. This was never found as seedling during summer, but after winter rains it was very abundant everywhere. Under this name also some *Stylocline* species are included, which as non-flowering plants were hard to separate.

5. *Gilia* species. These germinate only after winter rains. As a single exception one plant of *Gilia virgata* Steud. var. *ambigua* Craig was found flowering in the Mojave Desert near Cajon Pass, at 1200 m. altitude, on October 25, 1946. This plant was obviously not more than 2 months old, and therefore had germinated about September 1. Since the plant looked healthy it seems as if moisture and temperature had been well within the tolerance limits of this plant, and others

could have grown too, as they will in winter. Therefore, this one germination must have been an exception. All other *Gilias*, like *Gilia aurea* Nutt., were only observed in winter and spring.

6. *Lepidium lasiocarpum* Nutt. was found germinating after autumn and winter rains, but also after the August 16-17, 1947, rain in Hidden Valley. On September 6, 1947, these plants had very small rosettes, and therefore this species might almost be listed in the next group.

7. *Nemacladus*. Only in December 1945 and January 1946 were any seedlings of this plant observed. This seems to be one of the strictest winter annuals.

8. *Plantago*. Although occasionally seedlings were found in late summer (September 23, 1945, at Quail Springs), the majority of seedlings appeared in winter (November and December 1945).

Summer germinating spring annuals

There is a small group of annuals which flower in winter or spring, but which germinate in late summer. These are usually the larger spring plants.

1. *Abronia villosa* Wats., the sand verben. This was found germinating in September 1945 and again in August 1946 and September 1947, in the Hidden Valley area. Due to the repeated rains in August and September 1945, the plants grew very rapidly and flowered before winter. Usually they are found flowering from December on. This is the earliest annual to flower in the Palm Springs area, and it continues flowering as long as there is moisture.

2. *Erodium cicutarium* (L.) L'Her. This is a very common plant, with a very wide vertical distribution. It was found germinating abundantly after summer rains in August and September 1945, in the Hidden Valley area, and after winter rains in the Palm Springs area. It remained vegetative in the rosette stage until February, when flowers were formed. This plant seems to have a germination temperature which lies between that of the summer and spring annuals. It was

found germinating in small numbers in September 1947 in Hidden Valley and Pinto Basin.

3. *Oenothera deltoides* Torr. et Frem. Seedlings were found in September 1945 in the Quail Springs area. In general this species is so large when it flowers in spring that it must germinate after late summer rains. This is true for some other *Oenotheras* as well. E.g. *Oenothera clavaeformis* Torr. et Frem. germinated in the Cottonwood Springs area of the Joshua Tree National Monument after a small cloudburst in September 1946 (see fig. 2), and flowered there in March 1947, but only in the area of the cloudburst mapped. In the same area not a single *Oenothera* seedling was found after the rain of August 7, 1947. *Oenothera* seedlings found in the Pinto Basin on November 25, 1945, were probably *O. clavaeformis*.

4. *Salvia Columbariae* Benth. This was found as small seedlings on September 1, 1945, and September 7, 1947, in the Hidden Valley area, and these seedlings were observed on all subsequent trips in the 1945 season, growing slowly and withstanding the winter cold. In November and December 1946, seedlings were again observed in that area, and when transplanted into a cool greenhouse they flowered in April 1947. Until February they had remained in the rosette stage. No *Salvia* were found to germinate after winter rains in the Hidden Valley area.

Plants unrestricted in time of germination

1. *Cucurbitaceae* as *Brandegea Bigelovii* (Wats.) Cogn. and *Cucurbita palmata* Wats. were observed as seedlings at any time of the year, in the Pinto Basin. They are killed by frost and consequently they are found as flowering plants only in summer.

2. *Datura meteloides* DC. and *D. discolor* Bernh. Although these plants are killed by frost, seedlings may be found in spring as well as in summer and autumn after rains. Most observations of these plants were made in the Pinto Basin,

where it is common in the bottom of washes, and flowers in summer and fall.

3. *Palafoxia linearis* (Car.) Lag. This plant was found at almost any time germinating and flowering, especially in the Pinto Basin. It actually may grow as a perennial when the rains are frequent enough; its base will then become woody. Apparently *Nicolletia occidentalis* Gray behaves like *Palafoxia*, only it is a more pronounced perennial.

Germination of desert shrubs

With the germination of annuals, that of perennials and shrubs was observed simultaneously. The number of young seedlings observed in spring (or winter)

was very small, and essentially only several *Eriogonum* species, including annual, perennial and shrubby, were found then. *Eriogonum fasciculatum* Benth. is common in the Hidden Valley area, and is a chaparral rather than a desert shrub. Seedlings a few months old were found in May 1945 and June 1946; in late summer only well-established young plants were seen. Probably the whole genus *Eriogonum* is winter-germinating.

All other shrubs were observed germinating only in August and September 1945 and August 1946. The following gives a summary of observations in the Joshua Tree National Monument as well as in other desert regions.

Acacia Greggii Gray

Chilopsis linearis (Cav.) Sweet

Dalea spinosa Gray

Encelia farinosa Gray

Fouquieria splendens Engelm.

Franseria dumosa Gray

Hymenoclea Salsola T. et G.

Hyptis Emoryi Torr.

Larrea divaricata Cav.

Lycium Cooperi Gray

Olneya Tesota Gray

Sphaeralcea ambigua Gray

Yucca brevifolia Engelm.

many seedlings everywhere in vicinity of old shrubs

in washes in sand

in sandy washes

seedlings in sandy places

in immediate vicinity of old shrubs; did not survive, kept alive in greenhouse for ½ year

common in open spots. Germinates also at other times of the year

irregularly spread over open spaces

seedlings only in wash

seedlings in sandy places

many seedlings close to parent shrubs

seedlings only in wash

seedlings in sandy places

seems to germinate any time after a rain after shedding of the seed, which occurs in summer. Because the seeds are eaten by rodents, they have a chance to germinate only immediately after shedding or when they have been buried or lodged in an inaccessible place.

All these plants have extensive root systems, which enable them to survive long periods of drought. Seedlings have little chance for survival unless they can develop relatively large root systems before the dry season starts. This is accomplished in two ways:

1. Seedlings of perennials usually grow only a little above ground the first few

months after germination, but send down a very long taproot. Seedlings of *Dalea spinosa*, two months old, are usually not higher than 3 cm., with a few leaves and the first small spiny branches, but their roots are well over 40 cm. long. Once they are well developed in permanently moist soil regions, the tops grow faster. In annuals usually a small but spreading

root system is formed in a month, which penetrates only superficial soil layers with their temporary moisture.

2. Deserts in Southern California have winter rains regularly, but occasional cloudbursts occur in summer. Germination after an occasional heavy rain in summer makes it possible for the seedlings to utilize the reliable winter rains especially in extensive root development, and then have a whole spring season for further growth before the long drought sets in.

GERMINATION BEHAVIOR IN THE LABORATORY

For an understanding of these observations it is necessary to mention some of the results of germination experiments, to be reported in detail in later publications in this series. These are presented in table I. It shows the conditions under which some of the desert plants discussed above can germinate. In the first place there are plants, exemplified by *Pectis*, which will not germinate unless the seeds are leached for a considerable time in running water, due to water-soluble seed inhibitors present in them. A prolonged rain will do the same thing; therefore *Pectis* can only germinate after a heavy rain. In addition the temperatures have to be high, since no germination occurs at 20° C. or below. *Amaranthus fimbriatus* has the same temperature requirements, but will germinate without leaching. *Baeria chrysostoma* F. et M. germinates only at low temperatures, and therefore occurs only after winter rains. *Palafoxia*, which belongs to the plants unrestricted in time of germina-

tion, actually germinated at any temperature tested. *Cercidium floridum* Benth. germinates only after the seedcoat has been broken, which in nature occurs in washes after heavy rains due to the grinding action of sand and stones. In *Dalea spinosa* the seeds remain in the pods when they drop off the shrub. The presence of the pod completely, and of the seedcoat partially, inhibits germination, so that this plant also germinates in washes after heavy rains only, when sand and stones moving down the wash have ground off pod and seedcoat.

DISCUSSION

The vegetation of annual plants in the Joshua Tree National Monument and surrounding regions shows great variation from place to place, from season to season and from year to year. Part of this variation is due to differences in rainfall: only after rains of more than 20 mm. does germination occur. Local differences in rainfall, especially during summer, cause the local development of certain plants, with usually very sharp boundaries of the areas where they occur.

The seasonal differences in vegetation are perhaps even greater, for there are very few annuals which are found growing the year around. There is a complete separation between summer and spring annuals; the former occurring during July, August and September, the spring annuals growing between November and May. The observations made allow drawing the following conclusions:

1. Summer and spring annuals differ fundamentally in one respect: their time

TABLE I. Germination conditions for some desert plants

| | Leaching by running water | Scarification by breaking seed coat | Germinating at | | | | | |
|------------------------------|------------------------------|---|----------------|-----|-----|-----|-----|----|
| | | | 30° | 25° | 20° | 15° | 10° | 5° |
| <i>Pectis papposa</i> | over 24 hours | unnecessary | ++ | ++ | + | - | - | - |
| <i>Amaranthus fimbriatus</i> | unnecessary | unnecessary | ++ | ++ | - | - | - | - |
| <i>Palafoxia linearis</i> | unnecessary | unnecessary | + | + | + | + | + | + |
| <i>Baeria chrysostoma</i> | unnecessary | unnecessary | - | - | + | ++ | ++ | ++ |
| <i>Yucca brevifolia</i> | unnecessary | unnecessary | | ++ | ++ | | | |
| <i>Cercidium aculeatum</i> | unnecessary | essential | | ++ | ++ | | | |

of germination. No *Pectis* was found to germinate in winter or spring, whereas no *Nemacladus* or *Gilia* was found as seedling in summer. Their further growth is not so exclusively limited to either summer or winter, as shown by the one *Gilia virgata* growing from August to October 1946, or the resprouting of old rosettes of *Bouteloua barbata* and *B. aristidoides* in winter, or the few small flowering plants of *Eriophyllum* growing in October–November 1945. In other cases, such as the summer-germinating spring annuals, the optimal germinating and growing conditions differ very much, germination occurring at much higher temperatures than growth.

2. Germination was only observed after heavy rains, whereas after light rains no seedlings were found. For *Pectis* and many other summer annuals, 10 mm. of rain is not sufficient to make them germinate. At least 25 mm. is needed; this figure probably varies with the species, and this may partially explain the occurrence of certain plants in some years but not in others. In gullies where even after a light rain some water may accumulate, germination of *Pectis* and *Bouteloua* can be observed after as little as 10 mm. of rain, when on the flat areas of the desert not a single seedling is to be found.

3. The largest specimens were found when germination occurred after a very heavy rain or when within a few weeks after germination other rains occurred. This is not merely a question of available water, for after heavy rains the plants remain vegetative for a long time, and start to flower only after a considerable size is reached. After the lightest rains which just allow germination, the plants almost immediately change over to the reproductive stage, and thus remain diminutive. This may be due to differences in root development.

4. When germination has been limited due to little rain or due to low temperatures following heavy rain, the resulting vegetation of annuals is very sparse. But in these cases one usually finds no pre-

mature dying, and each germination is reflected in a flowering plant some weeks or months later. When germination has been very heavy, and later growing conditions are poor, due to lack of further rain, most of these seedlings survive, and a vegetation of numerous depauperate plants results, each one producing at least one flower and one seed. This means that the final vegetation of annuals is solely a reflection of their germination or, in other words, that germination-control, and not subsequent survival of the fittest due to a struggle for existence, determines the floristic conditions of a vegetation of desert annuals.

5. By proper germination controls, desert annuals are able to circumvent the rigorous desert drought conditions. They grow only when enough water is present to carry them through flowering to seed ripening. By having flexible proportions they can flower when very small or when developed into a fair-sized plant, according to the availability of water. Tenfold differences in linear dimensions between individual plants are very common in desert annuals.

6. Whereas very few dying annual plants have been observed in this region in nature, the shrubs show a much greater degree of dying in their earlier development. The spacing of shrubs is rigorously controlled in the desert and ultimately only one new shrub can become established for everyone which dies. Since extensive germination of shrubs was observed during late summer, it follows that the distribution of desert shrubs is not controlled by germination, but by survival of seedlings and young plants. Actually a number of dying shrubs have been observed (e.g. *Dalea spinosa* in their second year, *Larrea divaricata* both in their first and second year).

7. The germination control of desert plants will be described in detail in later articles of this series, but from the field observations and the data of table I, it can be concluded that temperature, rain and the surrounding vegetation are all of

error. Verification in every instance involves minute, painstaking and repeated comparisons with corresponding structures from authenticated herbarium or museum specimens. Despite all the care that has been taken in the determination of the species recorded in the following pages, there are no doubt some mistakes. However, it is hoped that they are so few as not materially to affect the general picture.

The materials upon which the identifications rest are preserved in the paleobotanical collections of the Department of Botany.

In the preparation of this paper, I have had valuable help from many of my colleagues, former graduate students and a number of persons outside academic circles who have taken a keen interest in the work. Dr. A. E. Jenks, former head of the Department of Anthropology of the University of Minnesota, secured all of the rich material from the Bronson site. He was present during the drilling operations and prepared a complete log of the well. Dr. C. O. Rost, Head of the Division of Soils in the College of Agriculture, discovered most of the plant-yielding road cuts of the southern part of the state and he accompanied me to the different sites on several collecting expeditions. Professor C. A. Ballard, former Head of the Department of Biology of the Moorhead State Teachers College, obtained material and data from the Lake Agassiz deposit. Dr. Samuel Eddy secured the material from the marl bed at Nye (Wisconsin), and Mr. Ludwig Kelnauf from the Jackson well. Dr. C. R. Stauffer and Dr. G. M. Schwartz of the Department of Geology of the University of Minnesota have from time to time submitted material obtained on their geological survey expeditions in various parts of the state. Much fine wood material from the Springfield deposit has been furnished by Mr. C. W. Blue, foreman for the A. C. Ochs Brick & Tile Company of that place, and thanks are due Mr. Ochs, President of the Company, for

permission to explore the extensive shale pits on several occasions.

In the work of preparing the material for examination and microscopic study I have had the help of several former graduate students. Dr. Robert R. Humphrey sorted all the material from the Bronson well and prepared slides of a great many wood samples. He also made tentative identifications of some of the material. Dr. Margaret Dudley prepared the slides of the wood obtained from a majority of the other stations. Other graduate students who have aided are Dr. Etla Nielsen, Dr. George Burns, Mr. Edward Thatcher and Dr. A. O. Dahl. To Dr. W. C. Steere I am greatly indebted for the laborious task of identifying the mosses, all of which he named except one species subsequently found and submitted to the late Dr. A. J. Grout. Eighty-five of the pen and ink illustrations were prepared by Mr. Ludwig Kelnauf, one by Mrs. J. W. Moore and the remaining ones by Miss Wilma Monserud.

To all who in one way or another have so generously helped I wish to express my sincere appreciation and cordial thanks.

EARLY DISCOVERIES AND SITES

The first published account of the occurrence of plant remains of Pleistocene age in Minnesota is given by Dr. N. H. Winchell (1875a) in the Third Annual Report of the Geological and Natural History Survey of the state. The report is based on the presence of a layer of "muck containing sticks" encountered at a depth of 38-40 feet in wells in the region of Albert Lea in Freeborn County. Winchell stated that the muck layer may indicate a former bed of the river or an interglacial marsh as "James Geike had explained in Scotland." That he was somewhat skeptical about the latter possibility is clear from his subsequent statement that since the layer "seems not uniformly to hold sticks and leaves but to be rather a fine sand of dark color," he expressed the opinion that it was either

a bed of Cretaceous clay, arenaceous, or Cretaceous debris. Further on in the same report he related the discovery of a bed of vegetable material having the appearance of peat but containing some coarse pieces of fibrous wood, outcropping in the bank of Rose Creek in the southeast quarter of Section 12 of Windom Township of Mower County. The site is 8 miles due east from the city of Austin. The layer where it outcropped was only about half an inch thick and was stated to consist of comminuted vegetable fiber. Excavations carried on by a resident of the locality revealed that the bed or layer had a nearly horizontal drift and at a distance of 70 feet from the stream bank it had a thickness of 18 inches. In the course of excavation pieces of wood, judged to be cedar and pine, one of which measured 2 feet in length and 10 inches in diameter were found at the top of the peat bed. Above the peaty layer there was "blue clay with gravel stones and below it a dark blue clay with gravel stones." Winchell concluded his account of this deposit as follows: "This peat seems to have been in a genuine ancient peat lake, filled or partly filled, on which floated pieces of wood from the surrounding forest. The whole was buried again by glacial deposit 50 feet thick." Dr. Winchell's lively interest in the discovery led him to further investigations, especially as to the possible wider occurrence of the peat bed in this particular area of the state. Through information obtained from farmers and professional well drillers, it was disclosed that over a considerable portion of eastern Mower County and into adjoining Fillmore County there was present a buried vegetable layer, varying in thickness from 2 to 8 feet. In all instances the peat deposits were stated to be immediately overlain with blue clay, and variously underlain with blue clay, gravelly blue clay, black clay or gravel. These facts are briefly recorded in the Fourth Annual Report for the year 1875.

In the same year Winchell (1875b) presented before the Detroit meeting of the American Association for the Advancement of Science a paper entitled "Vegetable Remains in the Drift Deposits of the Northwest" wherein he summarized the reports of the occurrence of such deposits in Ohio, Indiana, Illinois, Wisconsin and Minnesota. In addition to the deposits in Mower and Fillmore Counties referred to above he reported additional stations in Freeborn, Scott and Wilkin Counties in Minnesota. In contrast to the relatively shallow position (30-50 feet) of the peat beds in the southeastern counties of the state the material from Belle Plain in Scott County, identified as pieces of grape vine, was found in gravel and sand at a depth of 168 feet, while that from Wilkin County in the southern part of the Red River Valley, said to resemble cedar, occurred at 173 feet below the surface.

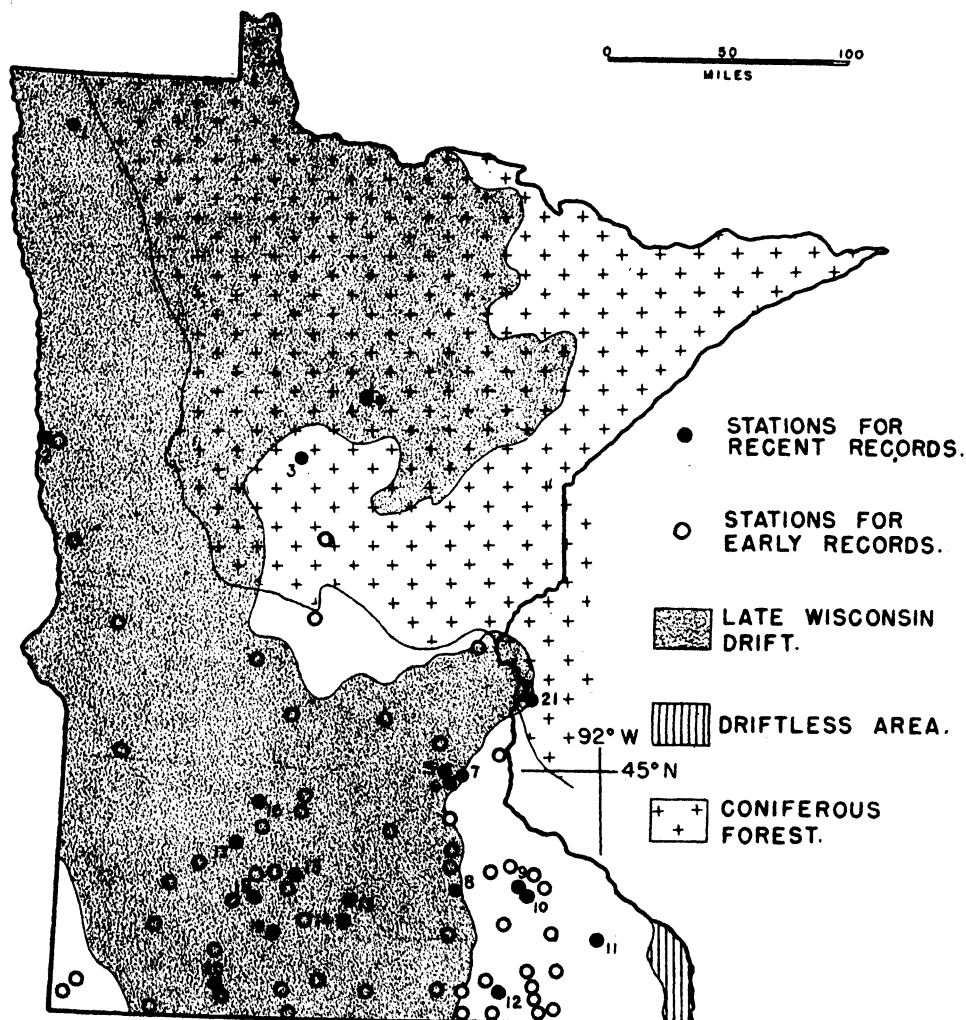
During the next 24 years of active prosecution of the Geological Survey of Minnesota many additional stations for Pleistocene plants were reported so that by the time the 4th volume of the Final Report was published in 1899 over fifty separate stations had been recorded, distributed over thirty-four counties of the state (see map).

Aside from showing that ancient plant remains were of frequent occurrence in the drift and widely distributed in the state these early finds contributed little in the way of definite knowledge, first as to the interglacial interval to which they belonged and second as to the number and identity of the plant species represented in the material recovered. It is true that most of the records antedate the time when the different drift sheets had been sufficiently clearly recognized and differentiated and any definite assignment could therefore not be expected. The fact that most of the material came from wells at depths ranging from 10 to 195 feet and that the information regarding the strata in which they occurred was supplied by farmers and well drillers

would render subsequent attempts to refer any of them to one or another of the recognized interglacial intervals well nigh futile. The only exception would be in the case of the peat deposits in Mower County but even in regard to the age of these, eminent students of the Pleistocene have held widely divergent opinions. Winchell (1876) stated that they occur

between the two old drift sheets and Chamberlin (1895) supported this interpretation by referring them to the Aftonian interglacial.

Baker ('20) on the other hand, in discussing Minnesota plant remains in his "Life of the Pleistocene," expresses the opinion that the 6-8 feet thick peat deposits in Mower County belong to the



MAP. The Pleistocene deposits on which this paper is based are located at the places marked on the map by the solid circles. The stations are numbered as follows: 1 **Bronson**, 2 **Moorhead**, 3 Backus, 4 Boy River, 5 Minneapolis, 6 Bloomington, 7 St. Paul, 8 Faribault, 9 Zumbrota, 10 Pine Island, 11 St. Charles, 12 Rose Creek, 13 Mankato, 14 Garden City, 15 New Ulm, 16 Bird Island, 17 Redwood Falls, 18 **Springfield**, 19 St. James, 20 **Jackson**, 21 **Nye (Wisconsin)**. The stations printed in boldface type have provided the most complete records.

Yarmouth interval, occurring, as he states, beneath 50 feet of Iowan drift. The lack of any convincing evidence of the occurrence of such an extensive deposit of Iowan till in this particular area of Minnesota makes it extremely doubtful if any of the Mower County deposits are of Yarmouth age. Upham ('13) regards them of still later origin and assigns them to the Sangamon interval. In the light of the interpretation of Leverett and Sardeson ('32) that the surface drift of the region is Kansan, it is obvious that Upham's view is untenable.

More recent investigations by Nielsen ('35) on the previously mentioned peat deposits in the banks of Rose Creek fully corroborate Chamberlin's interpretation, for he found the peat bed to be situated between unmistakable Nebraskan till below and Kansan till above.

The woody material recovered from the early discovered deposits in the form of logs was variously reported to be cedar, pine, tamarack, oak, elm, poplar, cottonwood, willow, and grape vine. At other times the plant remains were merely stated to be pieces of wood, sticks, leaves, grass, or layers of peat. From the fact that none of the material is any longer extant, it appears likely that no special effort was made to assemble and preserve it for detailed study. At least there is no evidence that the logs and pieces of wood were examined microscopically for verification of the purported species nor that the material from the peat deposits was minutely studied for the kinds of mosses, fruits, seeds and spores they might contain. However, neglect of specific identification was characteristic of much of the early work on Pleistocene plant remains in this country and it should not be charged up as merely a local shortcoming. As a matter of fact no thoroughgoing study of Pleistocene deposits with a view to identification of species was done in America until the outstanding work by Coleman (1894) and Penhallow (1896) during the middle nineties of the nineteenth century.

By the turn of the century exploration and investigation of the mineral resources of the northern part of Minnesota had assumed such overshadowing importance that the energies of the Geological Survey of the state were largely directed toward this end. Matters of such non-practical nature as plant remains buried in the drift ceased to attract attention and one looks therefore in vain in publications of the Survey or in other sources for any further reference to them. This sterile period was destined to last almost a quarter of a century and local interest was first revived by the discovery of a rich Pleistocene deposit in the environs of Minneapolis in 1923. The materials recovered from this deposit were studied by W. S. Cooper and some of his graduate students and the results of their investigations were published in *ECOLOGY* (Cooper and Foote, '32). In addition to recording several species not previously reported from the Pleistocene in North America, this paper was also the first one in which the reconstruction of a Pleistocene biotic community was attempted. The publication was important in another respect in that it reawakened a keen interest in the study of interglacial plant deposits which at this juncture began to be reported from various parts of the state as a result of extensive construction projects, both state and federal, which got under full headway during the depression years. Several of these undertakings involved the making of deep cuts and excavations in some of which the succession of till sheets was so clearly revealed that the interglacial intervals to which the deposits belonged were practically beyond doubt. More than a score of new sites, including deep wells, have been located during the last fifteen years and the present contribution is the result of a study of the materials brought together during this period.

Of the stations from which the materials have been critically studied for their macrofossils, five have yielded eight or more species. From most of the others only

a single species (*Picea glauca*) has been obtained. The material ranges in age from early to late Pleistocene. Where it was derived from wells with scant or untrustworthy data as to the nature and composition of the till, it has obviously been impossible to refer it with any degree of certainty to any one of the interglacial intervals. On the other hand, where it came from deep cuts and excavations or wells where a complete log was kept and in addition samples of till were secured, it has appeared reasonably safe to assign it to a definite period. Fortunately, these conditions obtained for the five stations (1, 2, 18, 20, 21) from which a majority of the species emanated.

NEW SITES

Stations² with several to many species

Moorhead, Station 2, Late Pleistocene.

—The vegetable deposit at Moorhead was discovered in the course of excavating for a sewage disposal plant located on the banks of the Red River, a few yards back from the edge of the stream. According to a local observer it was encountered at a depth of about 25 feet and the overlying material consisted of alternating light and dark layers (varves) of Lake Agassiz silt. There were over 1800 of these alternating layers. The present banks where the excavation was made are an estimated 20 feet below the flat surrounding country (Lake Agassiz bottom) so that the number of varves which originally covered the vegetable stratum must have been much greater. The plant-bearing deposit was nearly 2 feet thick and sloped from N.E. to S.W. with a dip of about 8°.

The mixture of wood, bark, sticks, stumps and other plant debris was of such a nature as to preclude the possibility of growth in situ. It appears likely that the material came from the beaches and moraines 15–20 miles to the east and may

have been carried into the lake by the Buffalo River which cuts through the moraines due east of Moorhead. The dip of 8° of the plant stratum possibly indicates a corresponding slope of the ground moraine at that particular spot. Leverett and Sardeson ('32) estimate that the River Warren subsided some 8000 to 9000 years ago, marking the end of overflow southward by Lake Agassiz; and that the beginning of Lake Agassiz dates back about 18,000 years. Considering the depth at which the Moorhead deposit was found, it is safe to assume that it was laid down fairly early in the history of the lake and that it may be 12,000 to 15,000 years old.

The following species have been identified from the Moorhead deposit:

ALGAE

Cladophora sp.

FUNGI

*Rhizophagites Butleri*³

Fomes sp.

BRYOPHYTA

Cratoneuron filicinum

Drepanocladus aduncus

D. fluitans

D. minnesotensis

Mnium affine

PTERIDOPHYTA

Equisetum arvense

GYMNOSPERMAE

Larix laricina

Picea glauca

ANGIOSPERMAE—MONOCOTYLEDONAE

Potamogeton foliosus

P. Richardsonii

P. zosteriformis

Sagittaria cuneata

Cyperus crythrorhizos

Eleocharis acicularis

E. intermedia

E. patustris

Scirpus acutus

S. validus

Carex Bebbii

C. disperma

C. synchnocephala

² The deposits are treated in chronological order beginning with the youngest. The location of the different stations, each named for the nearest city or village and numbered, is shown on the accompanying map.

³ See Rosendahl, '43.

C. rostrata

Juncus canadensis

ANGIOSPERMAE—DICOTYLEDONAE

Populus balsamifera

Rumex persicarioides

Polygonum lapathifolium

P. amphibium

P. ramosissimum

Chorispermum hyssopifolium

Ranunculus delphinifolius

R. Purshii

Potentilla norvegica var. *hirsuta*

Hippurus vulgaris

Vaccinium angustifolium

Fraxinus pennsylvanica

Bidens cernua

The species listed are all characteristic components of the present day flora of the region. As already suggested, the plant materials must have been deposited in the early stages of Lake Agassiz and it is reasonable to assume that the invasion by these species followed close upon the retreat of the ice front. It is significant that none of the species found are tundra plants and there is no supporting evidence for assuming a tundra stage in the revegetation of the area.

Nye, Wisconsin, Station 21 Late Pleistocene.—This deposit, judged to be about the same age as the one at Moorhead, is located a short distance east of the St. Croix River near the village of Nye in Polk County, Wisconsin. The site is a peat bog underlain with a deep deposit of marl which was opened for the purpose of obtaining marl for liming the highly acid farmland of the region. The bog is situated on middle Wisconsin (Cary) drift a few miles beyond the southern limit of the Grantsburg lobe of the late Wisconsin. Numerous pieces of wood were obtained at depths of 6–10 feet in the marl, commingled with great quantities of bones (Eddy and Jenks, '35) of elk, caribou and an extinct species of bison (*Bison antiquus*). According to Dr. Samuel Eddy (personal communication), fully 90 per cent of the exhumed bones belonged to the last named species. The woody plants

found in the marl are *Salix* sp., *Populus* sp., *Alnus incana*, *Quercus alba*, *Q. borealis*, and *Ulmus americana*. Two of the sticks of white oak, each about 2 inches in diameter, were gnawed by beavers with the teeth marks clearly visible at the cut ends. The presence of two species of oak and the common elm in the deposit indicates sufficient amelioration of the climate to permit the readvance of a hardwood forest into the area during the waning stages of the Pleistocene. In addition to the woody material innumerable fruits of *Chara* and of *Najas flexilis* were recovered from the marl.

Jackson, Station 20, Peorian Interglacial (probable age 45,000–50,000 years).

—The deposit from the Jackson site is from a well situated about 2 miles northwest of the town. It was found at a depth of 110 feet but no data are available regarding the nature of the overlying till. The material consisted of several fairly large pieces of wood and a large number of fruits and seeds imbedded in lumps of dark clayey silt which were brought up in the bailing bucket. As regards number of fruits and seeds it is the second richest find hitherto recorded for the state and in number of species it ranks third. The species identified are:

ALGAE

Chara sp.

FUNGI

Rhizopogonites Butleri

BRYOPHYTA

Calliergon giganteum

GYMNOSPERMAE

Larix laricina

Picea mariana

P. glauca

ANGIOSPERMAE—MONOCOTYLEDONAE

Sparganium minimum

Potamogeton amplifolius

P. foliosus var. *macellus*

P. Freesii

P. pusillus

P. pectinatus

P. praelongus

P. Richardsonii

Najas flexilis
Sagittaria latifolia
Eleocharis calva
Scirpus validus
Carex rostrata
C. trichocarpa
C. vesicaria

ANGIOSPERMAE—DICOTYLEDONAE

Populus balsamifera
Polygonum lapathifolium
Ceratophyllum demersum
Ranunculus subrigidus
Rubus strigosus
Viola nephrophylla
Myriophyllum exalbescons

This assemblage of species, ranging from true aquatics and lake shore plants to shrubs and trees, is abundant evidence that the site must have gone through stages of succession from open water to spruce-tamarack bog. The numerous species of *Potamogeton* together with *Chara*, *Ceratophyllum*, *Najas*, *Myriophyllum* and water *Ranunculus* reveal a pond or lake habitat fringed by such typical emergent aquatics as *Sparganium minimum*, *Scirpus validus*, *Eleocharis calva* and *Sagittaria latifolia*. A sedge mat stage in the succession is evidenced by the characteristic marsh sedges *Carex rostrata*, *C. trichocarpa*, and *C. vesicaria*.

Although the plant material from the Jackson County well was found at considerable depth in the drift, the available evidence favors assigning it to the last interglacial interval. Upham (1884) in his account of the wells of Jackson County reported the finding of wood and gastropod shells at a depth of 100 feet in a well in the village of Jackson. He stated that after 2 feet of soil the well was "all till, yellowish above but mostly bluish, inclosing dark sandy streaks but no considerable layers of sand or gravel and no water, and having throughout some admixture of stone and gravel, one boulder weighing about 50 pounds being found at a depth of 100 feet." As mentioned above the wood and shells occurred at this level. It should be noted that the well

was situated in the valley of the Des Moines River and that the surface where it was drilled is approximately 70 feet below the surrounding upland level.

In the railroad well at Heron Lake, situated 15 miles to the northwest of Jackson, something like a soil horizon was found at a depth of 125 feet. According to Upham (op. cit.) the well log recorded "Soil 2 feet; yellow till 13 feet; blue till 100 feet; yellow clay 10 feet; dark, hard, fine silt, like dried mud 16 feet; gray clay 21 feet; interstratified sand and gravel 21 feet," at which depth the well struck the quartzite. The layer of dark, hard, fine silt would seem to be a fairly deep lacustrine deposit compacted by the overlying thick layers of yellow and blue till. In the ten additional wells of Jackson County described by Upham (op. cit.), ranging in depth from 19 to 72 feet, no plant remains or soil layers were found. From the data at hand one would conclude that the last interglacial surface over much of Jackson County is overlain by at least 100 feet of late Wisconsin drift and that the plant remains so far discovered in the area are referable to the Peorian interglacial interval.

Bronson, Station 1, Peorian Interglacial (estimated age 50,000–60,000 years⁴).—By far the richest deposit of Pleistocene plants so far discovered in Minnesota was encountered in well drilling operations near the village of Bronson, Kittson County in the northwestern corner of the state.

Incidents connected with the discovery of the deposit and the train of events following upon it are of such interest as to merit a somewhat detailed account. In the first place a 3-inch well was drilled to a depth of 101 feet. It promised an abundant supply of water but in a short time the pump became completely clogged. Upon removal it was found that the valves

⁴ Although this deposit is referred to the same interglacial as that of the Jackson Station (No. 20), it is probably several thousand years older since the site is about 360 miles farther north.

were filled with moss and other vegetable debris. The pump was cleaned and re-installed but on a second clogging it was decided that it would be necessary to "blow out" the well.

Accordingly a narrow pipe line was introduced, reaching to the bottom of the well, and air pressure of 35 lbs. applied. The blowing operation brought to the surface chips, masses of moss, a piece of wood six inches long and slightly more than an inch in diameter, and two bones each bearing scratches and "saw marks." The piece of wood and the two bones (ribs) were submitted to the Department of Anthropology of the University for examination. The rest of the material was put aside, but unfortunately was carried away shortly afterward by local curio hunters. The two bones with "saw marks" found in association with plant remains of interglacial age caused considerable excitement. The well drillers made affidavit that the bones came from the well along with the other material during the blowing-out operation.

Indubitably they bore scratches and saw marks. They were submitted to a number of authorities but no one was either able or willing to identify them with corresponding bones of any living form.

Were they then of some Pleistocene animal⁵ and was the place whence they, together with the plant debris, emanated some ancient camp site or kitchen midden of interglacial man? There seemed sufficient ground for such a possibility to justify further exploration. Accordingly it was decided to sink a new and larger well in the immediate proximity in the hope of obtaining additional evidence. The new well was drilled three feet away from the old one. It was a 12-inch bore and was lined with a 12-inch casing. A

complete log was kept and soil samples were secured by the use of an auger bit at every foot interval to a depth of 28 feet. Beyond the 28-foot level samples were taken at 2-foot intervals. After penetrating 3 feet of black soil and 16-17 feet of Lake Agassiz bottom silt the bore struck boulder clay of the Wisconsin ground moraine. The hard boulder clay continued to the 66-foot level when alternating layers of gravel, blue clay and sand were passed through. In some of these layers small boulders were encountered. From the 80- to the 87-foot levels there was mostly gravel and sand with very little clay. At 88 feet a layer containing abundant fragments of lignite and wood, mixed with sand and clay, was struck. The vegetable-bearing layer rested upon a stratum of mixed clay and sand which at the 91 foot level turned to a tenaceous blue clay with occasional stones. The well was drilled to a depth of 107 feet and for the last 6-7 feet, only homogenous blue clay without stones or gravel was met. The nature of the material suggested a lacustrine deposit of an earlier lake. Drilling operations beyond the 91-foot level proved extremely difficult on account of the "creeping" of the blue clay and it became necessary to keep the 12-inch casing going down in pace with the drill. Beyond the 97-foot level the well ceased yielding pieces of wood and lignite and it was apparent that the plant bearing stratum had been passed and sealed off by the casing. The casing was thereupon pulled up to the 88-foot level and bailing operations started. The bailing was done by means of a slush bucket 4½ feet long and 10 inches in diameter, holding slightly over 18 gallons when full. Altogether 232 bucketfuls were bailed out and the slush screened through three superposed screens of 4-, 2-, and ½-inch mesh respectively. A great deal of vegetable material was recovered in the process, some of it imbedded in clumps of clay of various dimensions up to 6 inches in diameter, the rest in the form of wads of moss, innumerable pieces of wood and a general mixture of vegetable debris.

⁵ The bones were ultimately identified as ribs of *Sus scrofa*. Several bone fragments belonging to the same species were later found scattered about on the ground near the well and it appears likely that the ribs had been picked up and dropped in by children at some unguarded moment when the well drillers were not on the spot.

All of it was immediately put into strong cotton bags, tied, labeled, and put aside for shipment to the University. The same process was followed in respect to the soil samples obtained in the course of sinking the well. Practically all the fruits, seeds and mosses were recovered from the clumps of clay which were broken down by soaking in water and the plant remains separated from the silt by washing in containers made of fine-meshed copper wire screens. The position of the vegetable-bearing stratum overlain by some 20 feet of alternating layers of clay and gravel, nearly 50 feet of hard boulder clay, 17 feet of Lake Agassiz silt and 3 feet of black soil proves conclusively that it cannot be of later origin than the last interglacial. That it could belong to one of the earlier intervals is possible but hardly probable on account of the state of preservation of the wood as compared with like material from the known older sites in the state.

The following species have been identified from the Bronson well (station 1):

ALGAE

Chara sp.

FUNGI

Rhizophagites Butleri

Fomes (*pinicola* ?)

BRYOPHYTA

Aulacomnium palustre

Bryum bimum

Calliergon giganteum

C. stramineum

C. turgescens

Campilium stellatum

Ceratodon purpureus

Distichium capillaceum

Ditrichum flexicaule

Drepanocladus aduncus

D. fluitans

D. minnesotensis

D. revolvens

D. vernicosus

Eurhynchium strigosum

Mnium affine

M. punctatum

Neocalliergon integrifolium

Scorpidium scorpioides

Thuidium delicatulum

Tortella fragilis

PTERIDOPHYTA

Equisetum scirpoides

GYMNOSPERMAE

Larix laricina

Picea glauca

P. mariana

Pinus Banksiana †

ANGIOSPERMAE—MONOCOTYLEDONAE

Sparganium chlorocarpum

Sparganium eurycarpum

S. fluitans

Potamogeton filiformis

P. foliosus

P. interior

P. pectinatus

P. pusillus

P. Richardsonii

P. zosteriformis

Zannichellea palustris

Najas flexilis

Scheuchzeria palustris

Eleocharis calva

Scirpus acutus

S. campestris

S. validus

Carex aquatilis

C. aurea

C. festucacea

C. Haydeni

C. lenticularis

C. rostrata

C. stricta

C. trichocarpa

C. vesicaria

ANGIOSPERMAE—DICOTYLEDONAE

Salix discolor †

Populus sp. †

Corylus cornuta †

Rumex mexicanus

Rumex persicarioides

Polygonum lapathifolium

P. littorale

P. amphibium

Atriplex argentea

Ranunculus Purshii

R. subrigidus

† Identifications based on wood.

R. trichophyllus
R. trichophyllus var. *calvescens*
R. trichophyllus var. ?
Fragaria americana
Potentilla anserina
P. pennsylvanica var. *strigosa*
Prunus pennsylvanica
Acer spicatum †
Myriophyllum exalbescent
Hippurus vulgaris
Menyanthes trifoliata

That the site of the well was at one time a lake or a pond is attested by the abundance of fruits of such characteristic aquatics as *Potamogeton*, *Najas*, *Sarganium*, *Zannichellea*, *Myriophyllum* and aquatic species of *Ranunculus*. That it very likely was near the margin of such a lake or pond is suggested by the fruits of a number of emergent aquatics, viz. three species of *Scirpus*, *Eleocharis calva*, *Hippurus vulgaris* and in addition the moist lake shore species *Polygonum lapathifolium*, *P. littorale*, *Rumex persicarioides*, *Ranunculus Purshii* and *Potentilla anserina*. The occurrence of several mat-forming species of *Carex* (see list), together with abundant material of sub-aquatic species of the mosses *Calliergon*, *Drepanocladus* and *Scorpidium*, gives unmistakable evidence that in the course of succession a characteristic sedge mat was developed. The two typical bog plants, *Scheuchzeria palustris* and *Menyanthes trifoliata*, of which several seeds were found may well have been present in the sedge mat for it is the kind of habitat in which these two plants are most frequently encountered today in northern Minnesota.

The abundance and nature of the forest-floor litter recovered prove beyond doubt that the place was a typical spruce-tamarack forest at the time it was overwhelmed by the advancing glacier. The occurrence of the woodland mosses in thin sheets and their excellent state of preservation indicate that they were buried *in situ*. The larger pieces of wood also give no

evidence of having been transported in the morainic debris. They are not frayed or worn at the ends and many of them retained the bark intact. The remains of upland species, i.e. *Corylus*, *Populus*, *Prunus*, *Acer* and *Picea glauca*, in all probability were washed in from an adjoining ridge and had become incorporated in the forest litter before the site was buried.

In bailing from the 88-foot level of the well, quantities of lignite fragments were brought up mingled with the wood and other plant remains. The well drillers stated that they frequently had obtained coal from other wells in the region but never in such amount. It appears from the log of the Bronson well that the lignite must have emanated largely from the sandy-clay layers immediately overlying the stratum of plant remains for there is no trace of its occurrence in any of the samples taken at higher levels.

Noteworthy is the finding of charcoal in the vegetable debris. It is true that only a few small fragments were found but they are unmistakably charcoal and not lignite. Their presence seems hardly explainable on any other ground than the assumption of the occurrence of interglacial forest fires.

A considerable number of the stem and branch fragments of spruce which have been sectioned show a progressive decrease in the thickness of the annual rings toward the periphery. If this were only an occasional occurrence, little significance could be attached to it, but since it shows up in many different individual stems regardless of total age, and since there is a striking similarity in all of them, it virtually amounts to a climatic record. When growing under normal lowland conditions, spruce, as is well known, produces in the early part of the season a varying number of thin-walled cells of spring wood, after which the thick-walled cells of the summer wood are laid down. In the outer portions of the tree stems from the Bronson well, the annual rings show no summer wood (figs. 109-111). The growing seasons apparently became

† Identifications based on wood.

so short that only 2-5 rows of spring wood were formed during each of the last 20-25 years of the life of the trees. One finds a similar growth pattern in the trees growing near the permanent snow line in the high mountains and W. S. Cooper has observed the same phenomenon in a 400-year-old spruce which had grown in the proximity of the Columbia Glacier in Alaska (oral communication). The progressive refrigeration of the climate of northwestern Minnesota is therefore indelibly recorded in the trees that grew there at the time of the last ice invasion.

The excellent state of preservation of the mosses has already been mentioned. The most striking example of this is shown by one of the species of *Mnium* in which the plastids are still present⁶ (fig. 108). As a rule, species of *Bryum* and *Mnium* do not preserve as well as aquatic and subaquatic forms like *Calliergon*, *Drepanocladus*, *Camptothecium*, etc., for in the much older deposits, the former (to be dealt with farther on) are either lacking or occur largely as broken-down remnants whereas species of the latter genera retain the cell structure of the leaves intact.

In the Bronson well the woody material also shows little impairment from its long burial. Some of the larger pieces are often slightly flattened but for the most part the cell structure is either very little or not at all distorted. Neither is there any mineralization and the preparation of sections has not required any special treatment.

In respect to the preservation of Angiosperm leaves, on the other hand, the Bronson well deposit has proved disappointing. No single intact leaf has been recovered nor fragments large enough to offer a clue as to their identity. At most only small pieces, consisting of the skeletal network of veins, have been seen.

In marked contrast to this general deterioration of the leaves of the higher

plants is the well-nigh perfect preservation of the microscopic fungus *Rhizopogon Butleri*, mycelial clusters of which (fig. 101) were found in the mixture of mosses and forest-floor litter. The same fungus had been noted earlier by Butler ('39) in glacial clays from near Edmonton, Canada, and had been referred by him to the mycorrhizal endotrophic fungus *Rhizopogon*. Subsequently I (Rosendahl, '43) described the organism as a fossil under the designation *Rhizopogon Butleri*. The fungus was apparently of common occurrence during the Pleistocene for it was recovered from both the Moorhead and Jackson sites as already indicated (see stations 2 and 20). The material from each of the other sites shows the same remarkable preservation and it is difficult to comprehend how a structure as delicate as a fungus mycelium could have withstood without complete collapse the enormous pressure to which it must have been subjected.

It is noteworthy that the great majority of the plants found in the Bronson well deposit are the same species which occur in the region today. With the exception of the above mentioned fungus and the two mosses *Neocalliergon integrifolium* and *Drepanocladus minnesotensis* which are probably extinct and the arctic-alpine mosses *Distichium Capillaceum* and *Calliergon turgescens* which likewise are not known to occur at present, all the species listed are characteristic elements of the present-day flora of northwestern Minnesota. This strongly suggests that the climate which prevailed in the region during some time at least of the Peorian interval was much like the one of today. There is evidence, too, that edaphic conditions were similar. In the present Red River Valley flora, there are a number of species characteristic of brackish or alkaline soils, among which *Atriplex argentea*, *Potentilla anserina* and *Rumex persicarioides* are of frequent occurrence. Remains of these were found in considerable abundance in the Bronson deposit. The presence of the first-named species is

⁶ This phenomenon was also noted by Wilson ('32).

significant since it is typical of alkaline habitats over a wide area in the west, ranging from southern Saskatchewan eastward to northwestern Minnesota, thence southward through South Dakota, Nebraska to Colorado, Utah and California. It seems very unlikely that this species of the plains and the southwest could have migrated to northwestern Minnesota during the last interglacial and maintained itself unless the climate closely approximated the present one.

Springfield, Station 18, Pre-Nebraskan (Estimated age 1,000,000 years).—The site of the Pleistocene deposit at Springfield is located on the property of the Ochs Brick and Tile Company where brick and tile are manufactured from a stratified deposit of Cretaceous shale. The shale is underlain with a thin seam of lignite and immediately over it lies the dark and very compact Nebraskan till. The shale is in places 30–40 feet thick and at irregular intervals in it are horizontal layers of soft sandstone 2–4 inches thick containing in places abundant impressions of Dicotyledonous leaves belonging to the Dakota sandstone formation of the middle Cretaceous. In the process of stripping off the immediately overlying dark till, pieces of wood and other plant remains are frequently found imbedded in it and occasionally pieces of tree trunks 2–10 feet long and 5–10 inches in diameter are encountered.

The deposit of workable shale is dug with steam shovels and in one part of the pit this operation has exposed a preglacial gully eroded down to the stratum of lignite (figs. 113–114). The gully is filled with blue-black indurated Nebraskan till and along the line of contact between the till and the shale pieces of wood and other plant remains are found. Near the bottom of the till occur small lenses of peat up to 2 inches thick. There can scarcely be any doubt that this plant material dates back to early Pleistocene. In spite of its great age, however, most of it is in a good state of preservation. At the broken ends and in the cracks of the pieces of

tree trunks and branches there is generally a deposit of iron pyrite. Occasionally the resin ducts in the wood are plugged with a deposit of pyrite. Aside from this there is no other perceptible mineralization and the preparation of microscopic sections has presented no difficulty. Clumps of mosses are sometimes found partially imbedded in irregular nodules of iron pyrite but usually these can be broken open and the plants released. All the larger pieces of wood examined are spruce and the probability is that both white and black spruce are represented. Quantities of woody material in the form of twigs, chips, splinters, etc. still remain to be microscopically examined but tentative identifications have revealed nothing but spruce. Leaves of balsam fir occur occasionally as do partly broken-down cone scales of tamarack (fig. 87). Short shoots of tamarack are common (fig. 88). Mosses occur abundantly, either intermingled with other vegetable debris or else in thin layers in the lenses of peat mentioned above. In general the mosses characteristic of swampy or aquatic habitats, i.e. *Drepanocladus*, *Calliergon*, and *Camptothecium*, are well preserved, whereas others such as *Bryum* and *Mnium* are considerably disintegrated. Fruits and seeds of Angiosperms are relatively scarce in the Springfield deposit. Those which have been recovered are much blackened and fragile. Often they are partially broken down and in this respect they differ strikingly from the generally well-preserved fruits and seeds from the Bronson, Moorhead and Jackson stations.

The following species have been identified from the Springfield site (station 18):

FUNGI

Rhizophagites minnesotensis
*Trichothyrites pleistocaenica*⁷

BRYOPHYTA

Bryum bimum
Calliergon giganteum
Campylium stellatum

⁷ See Rosendahl, '43.

Camptothecium Woldenii^a

Drepanocladus fluitans

Distichium capillaceum

Ditrichum flexicaule

Hylocomium splendens

Hypnum patientiae

Mnium sp.

Scorpidium scorpioides

Tortella fragilis

GYMNOSPERMAE

Abies balsamea

Larix laricina

Picea glauca

P. mariana

ANGIOSPERMAE—MONOCOTYLEDONAE

Potamogeton pusillus

P. zosteriformis

Carex aquatilis

C. disperma

C. lenticularis

Stations with one or two species, rarely a few more

Unlike the foregoing station, none under this caption has yielded any fruits or seeds whatsoever. All identifications are based on woody material except in the single case of the Faribault Station (8) where pollens and spores were also utilized. The sites from which the plant remains were obtained are either wells or road cuts and sewer tunnels. Material from wells, brought up in slush buckets in the bailing process, is in the form of chips, broken twigs and miscellaneous wood fragments, whereas that from the road cuts consists of splinters, knots, and pieces of branches or stems up to 5 inches in diameter and 20 inches in length.

As regards the deposits from the wells, the question of which interglacial interval they belong to is largely a matter of conjecture since the only data supplied by the well drillers are those of depth at which they were found. In contrast to the problematic age of the well deposits, those from the cuts and excavations are referable to respective intervals without much of any doubt since it has been pos-

sible at such sites to distinguish the successive till sheets and furthermore to observe the structure and nature of the till in which the plant remains occur. The first five of the following described stations are all well sites and in light of the above explanation, the age assignments are perforce tentative.

Backus, Station 3, Peorian Interglacial (probable age 50,000 years).—Numerous fragments of a log of White Spruce (*Picea glauca*) were obtained at a depth of 89 feet. The wood showed little "aging" and it is likely that it occurred in the Patrician (Cary) drift of the Wisconsin glaciation.

Boy River, Station 4, probably Peorian Interglacial.—Two pieces of wood were found at a depth of 250 feet. One of these is White Spruce (*Picea glauca*), the other is Jack Pine (*Pinus Banksiana*). It appears likely that the material came from the same drift as that of the preceding station since the two are not far apart, both being located in a part of Cass County where there is a deep deposit of Patrician drift.

Bloomington, Station 6, Peorian Interglacial (probable age 50,000 years).—The site is in Sect. 29 of Bloomington Twp., Hennepin County. Several pieces of wood were brought up in bailer from a depth of 150 feet. Most of the pieces are White Spruce (*Picea glauca*), some probably Black Spruce (*Picea mariana*), and one piece of an undetermined species of willow. The sample also contained many fragments of lignite. The depth at which the material was obtained is nearly 50 feet below the present level of the Minnesota River bottom lands. The presence of lignites in the sample suggests that it may have come from one of the older drifts.

St. James, Station 19 (interval and age wholly uncertain).—Many small pieces of wood were obtained at a depth of 190 feet. Superficially the fragments are very similar and all those which have been sectioned for microscopic examination are White Spruce (*Picea glauca*). No data

^a Identified by A. J. Grout.

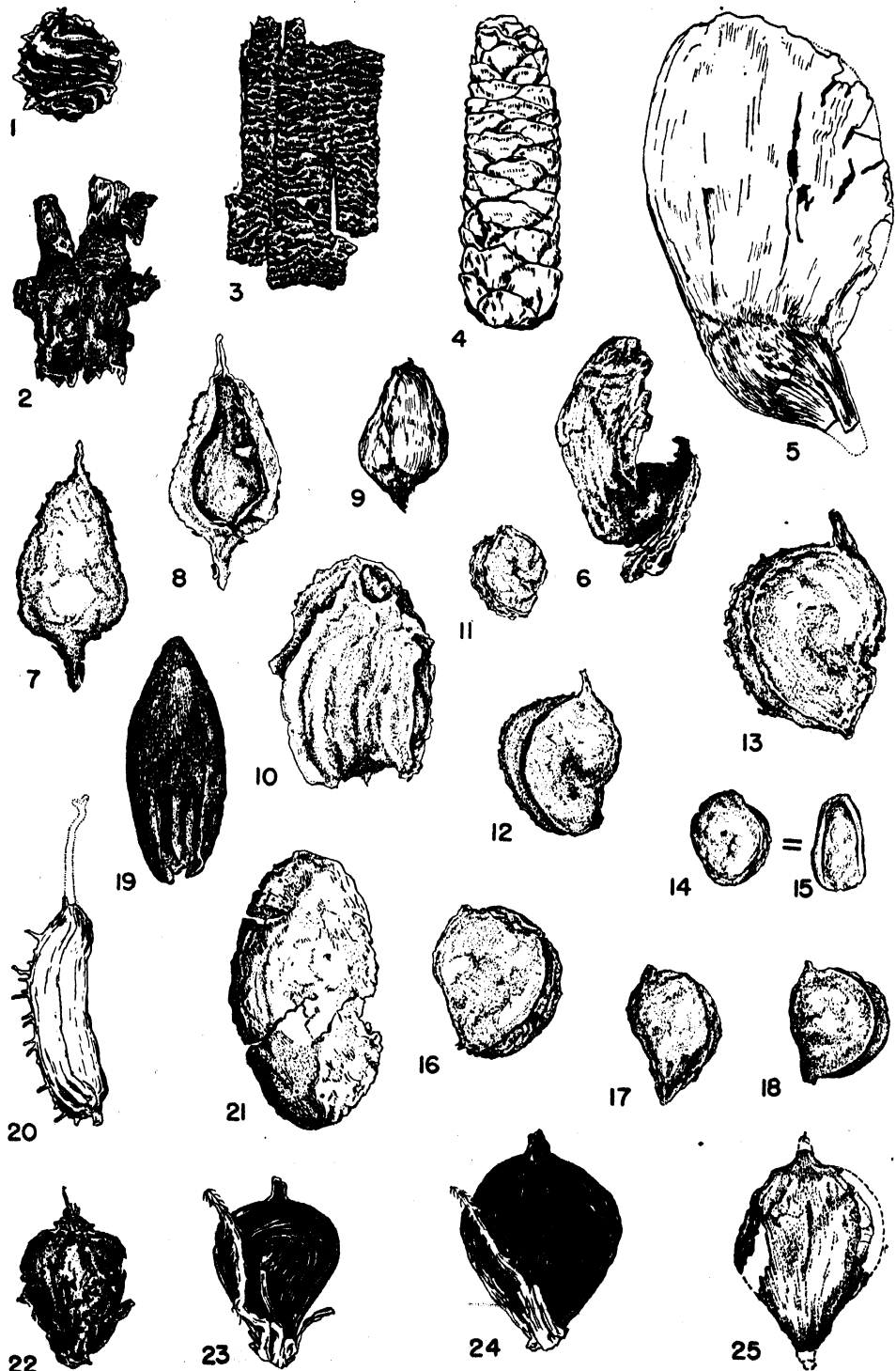


PLATE I

are available as to the probable drift in which the wood occurred.

Bird Island, Station 16, Aftonian (?) Interglacial (probable age 700,000 years).—The woody material from this well was found at a depth of 255 feet. This is the greatest depth for interglacial plant remains so far recorded in Minnesota. The material consists of a number of small twigs and several large chips of wood obviously broken off from a log by the drill. The slight curvature of the annual rings suggests a log of considerable size. Both twigs and chips are White Spruce (*Picea glauca*). In his discussion of the Geology of Renville County, Upham (1888) spoke of the presence of an "interglacial forest bed" inclosed in the drift over a considerable area near the center of Renville County, and he mentioned specifically the occurrence of logs and sticks in two wells in the Bird Island region. In one of the wells, the woody material was encountered at a depth of 20 feet, in the other at 39–40 feet. In both instances the wood was found in the upper part of a 4-foot stratum

of quicksand. In the deeper of the two wells the quicksand was overlain by a 2-foot layer of black loam. The drift above the loam was reported as consisting of 15 feet of blue till, 14 feet of yellow sand and above that 18 feet of yellow till. There can scarcely be any doubt that the plant remains in the two wells described by Upham are referable to the Peorian Interglacial while the recent find from more than 200 feet deeper in the drift of the same locality obviously belongs to one of the earlier intervals.

The desposits from the following 9 sites, all of which except one (station 7) are road cuts, date unquestionably far back into the Pleistocene. The cuts vary in depth from 12 to 55 feet and, when newly made, they clearly revealed the nature of the exposed drift. Three of the sites, viz. stations 9, 10, and 11, are well toward the edge of the Driftless Area, near the southeastern border of the state where the drift for the most part is thin, and where only the two oldest drift sheets are present. Stations 7 and 8 lie

PLATE I

Figures 1–60 incl. are of plants from the Bronson well (station 1)

- FIG. 1. *Chara* sp. Fruit $\times 24$.
- FIG. 2. *Equisetum scirpoides*. Node $\times 14$.
- FIG. 3. *E. scirpoides*. Part of flattened internode $\times 26$.
- FIG. 4. *Picea glauca*. Cone $\times 1$.
- FIG. 5. *P. Mariana*. Seed $\times 9$.
- FIG. 6. *Larix laricina*. Cone scale $\times 7.5$.
- FIG. 7. *Sparganium chlorocarpum*. Fruit $\times 8$.
- FIG. 8. *S. chlorocarpum*. Fruit, sectioned, $\times 8$.
- FIG. 9. *S. fluitans*. Fruit $\times 8$.
- FIG. 10. *S. eurycarpum*. Fruit $\times 7$.
- FIG. 11. *Potamogeton foliosus*. Fruit (endocarp) $\times 7$.
- FIG. 12. *P. Richardsonii*. Fruit (endocarp) $\times 7$.
- FIG. 13. *P. zosteriformia*. Fruit (endocarp) $\times 6$.
- FIG. 14. *P. pusillus*. Fruit (endocarp) $\times 7$.
- FIG. 15. *P. pusillus*. Dorsal view of same $\times 7$.
- FIG. 16. *P. pectinatus*. Fruit (endocarp) $\times 7$.
- FIG. 17. *P. interior*. Fruit (endocarp) $\times 7$.
- FIG. 18. *P. filiformis*. Fruit (endocarp) $\times 7$.
- FIG. 19. *Najas flexilis*. Seed $\times 12$.
- FIG. 20. *Zannichellea palustris*. Fruit $\times 8$.
- FIG. 21. *Scheuchzeria palustris*. Seed $\times 9$.
- FIG. 22. *Eleocharis calva*. Achene $\times 13$.
- FIG. 23. *Scirpus validus*. Achene $\times 12$.
- FIG. 24. *S. acutus*. Achene $\times 12$.
- FIG. 25. *S. campestris*. Achene $\times 9$.

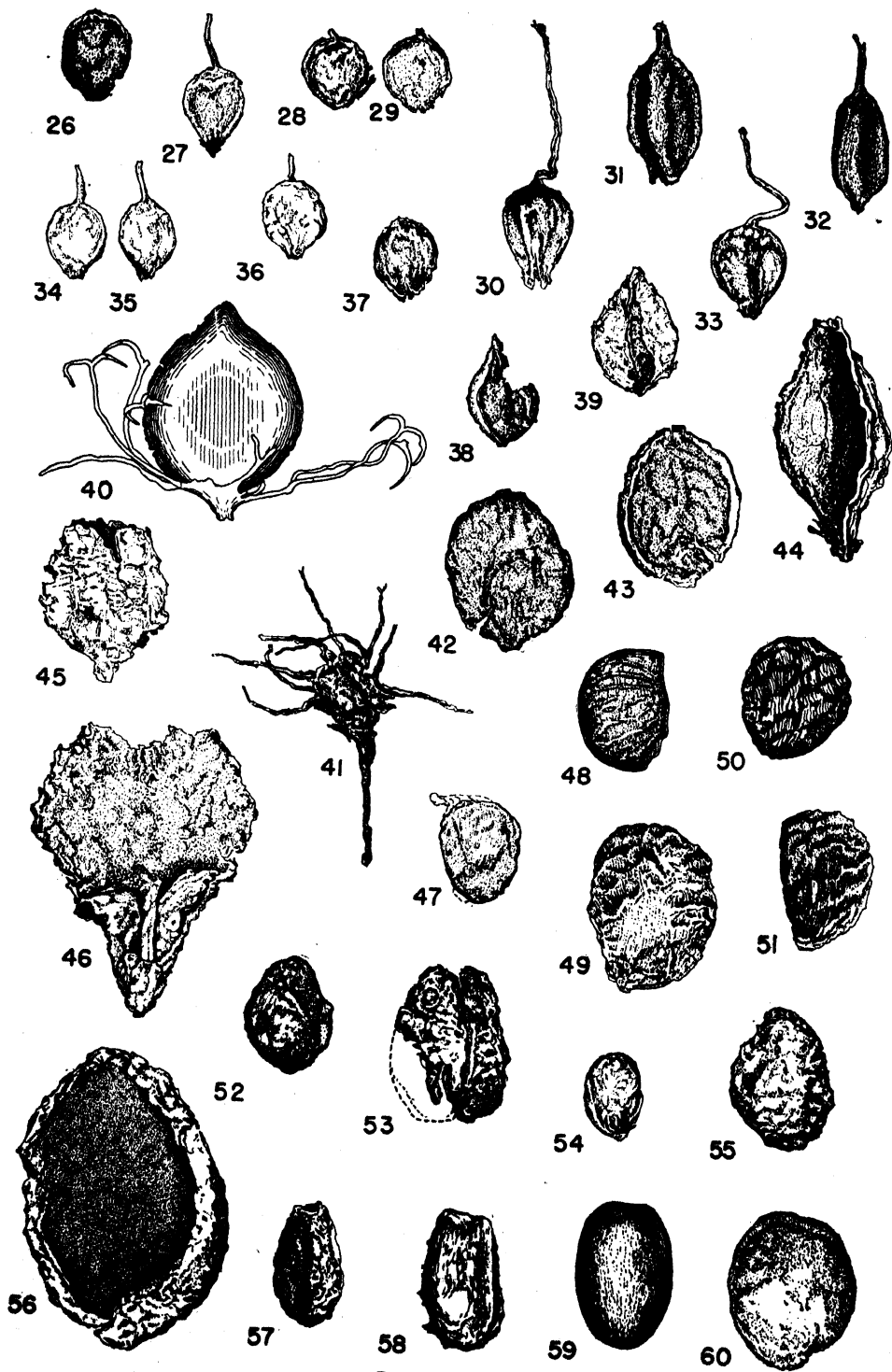


PLATE II

barely inside the eastern border of the late Wisconsin drift and stations 13, 14, 15, and 17 nearly midway between the eastern and western limits of the Des Moines lobe.

Faribault, Station 8, Aftonian Interglacial (probable age 700,000 years).— The site is a deep cut on the Chicago and Rock Island railroad, two miles southeast of the city. The plant-bearing layer here was discovered by Leverett and Sardeson ('32) who referred to it as "an exposure of a peaty bed between tills." Although the authors do not commit themselves as to which of the interglacial intervals the deposit belongs, the inference from the context is that they regarded it as Aftonian. In 1934 in company with Dr. Etlar Nielsen I visited the site and obtained samples of the peaty layer. It is largely made up of indeterminate vegetable debris with a consider-

able admixture of sand and clay but it also contains numerous chips and fragments of wood. The wood is mainly White Spruce (*Picea glauca*), but two undetermined woody dicotyledons are present. Microfossil studies were made on some of the peat, and pollen was found of Balsam Fir (*Abies balsamea*), spruce (*Picea*), Jack Pine (*Pinus Banksiana*), Maple (*Acer*), and a member of each of the families *Betulaceae* and *Chenopodiaceae*. Fruiting bodies of two microscopic fungi, viz. *Rhizophagites minnesotensis* and *Trichothyrites pleistocaenica*, also found in the Springfield deposit (see ante), are fairly common in the peat. Besides these two recognizable forms, there occurred spores and conidia of other fungi, attempts at identification of which have proved quite futile. This limited application of the microfossil technique at least shows that it can serve as a useful

PLATE II

- FIG. 26. *Carex festucacea*. Achene $\times 7$.
- FIG. 27. *C. aquatilis*. Achene $\times 8$.
- FIGS. 28 AND 29. *C. Haydeni*. Achene $\times 7$.
- FIG. 30. *C. rostrata*. Achene $\times 8$.
- FIGS. 31 AND 32. *C. trichocarpa* var. *aristata*. Achenes $\times 8$.
- FIG. 33. *C. vesicaria*. Achene $\times 7$.
- FIGS. 34 AND 35. *C. stricta*. Achenes $\times 7$.
- FIG. 36. *C. lenticularis*. Achene $\times 7$.
- FIG. 37. *C. aurea*. Achene $\times 7$.
- FIG. 38. *Rumex mexicanus*. Achene $\times 7$.
- FIG. 39. *R. mexicanus*. Achene $\times 7.5$.
- FIG. 40. *Polygonum lapathifolium*. Achene with attached perianth veins $\times 12$.
- FIG. 41. *Rumex persicarioides*. Fruit, showing bristly valves, $\times 8$.
- FIG. 42. *Polygonum amphibium*. Achene $\times 8$.
- FIG. 43. *P. amphibium*. Achene, broken open, $\times 7$.
- FIG. 44. *P. littorale*. Achene $\times 12$.
- FIG. 45. *Atriplex argentea*. Flower-subtending bract $\times 7$.
- FIG. 46. *A. argentea*. Mature bract, ventral view, $\times 7$.
- FIG. 47. *Ranunculus Purshii*. Achene $\times 10$.
- FIG. 48. *R. subrigidus*. Achene $\times 11$.
- FIG. 49. *R. trichophyllus* var. *Calvescens*. Achene $\times 11$.
- FIG. 50. *R. trichophyllus* var.? Achene $\times 11$.
- FIG. 51. *R. trichophyllus*. Achene $\times 11$.
- FIG. 52. *Potentilla anserina*. Achene, immature or seedless, $\times 9$.
- FIG. 53. *P. anserina*. Achene, with corky pericarp, $\times 9$.
- FIG. 54. *P. pennsylvanica* var. *strigosa*. Achene $\times 11$.
- FIG. 55. *Fragaria americana*. Achene $\times 13$.
- FIG. 56. *Prunus pennsylvanica*. Stone, broken open, $\times 9$.
- FIG. 57. *Myriophyllum exalbescens*. Achene $\times 8$.
- FIG. 58. *M. exalbescens*. Achene $\times 9$.
- FIG. 59. *Hippurus vulgaris*. Fruit $\times 11$.
- FIG. 60. *Menyanthes trifoliata*. Seed $\times 8$.

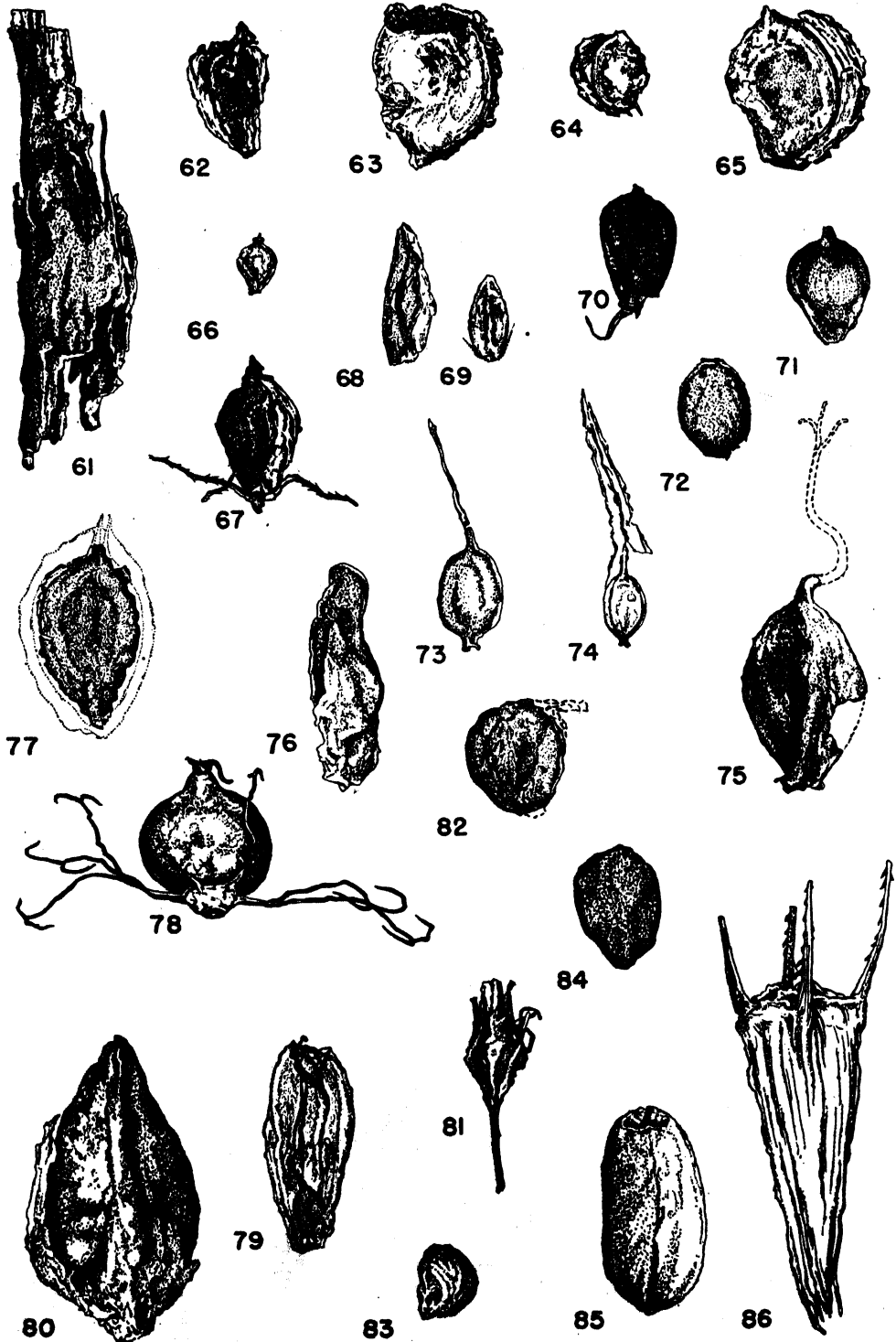


PLATE III

tool in the study of peat deposits of such great age as the early Pleistocene.

New Ulm, Station 15, and Redwood Falls, Station 17, Aftonian Interglacial (probable age 700,000 years).—The material from these two places was collected by Dr. Clinton R. Stauffer who reported it in both cases occurring in Kansan drift. I have not personally inspected the sites. The first of these is a road cut on Trunk Highway 15 on the south bank of the Cottonwood River a short distance below New Ulm. The wood which consists of several pieces of considerably flattened stems was obtained at a depth of 55 feet below the surface. The several pieces are White Spruce (*Picea glauca*). The second station is a cut on Highway 14, "near" Redwood Falls. The collection bears no data as to the depth at which it was found in the drift. All the pieces of wood are much flattened and are hard and blackened on the surface but otherwise in a good state of preservation.

All have been identified as White Spruce (*Picea glauca*).

*St. Charles, Station 11, Early Pleistocene*⁹ (probable age 700,000–1,000,000 years).—The St. Charles cut is located 2½ miles east of the village on U. S. Highway 14. It is about 14 feet deep and the wood occurs scattered throughout a 3–4-foot layer of blue-black till at the bottom of the cut. Only a few small-sized boulders are found in the layer but there are numerous small quartz pebbles and some limestone pebbles which crumble readily on slight pressure. I take this layer to be

⁹ The term *Early Pleistocene* is applied to deposits found imbedded in the Nebraskan till for instead of being wholly remains of a preglacial vegetation, incorporated in the till during the first invasion, they may possibly be of Aftonian age, worked into the underlying till by the next succeeding glaciation. Although the first of these two methods of deposition is the more likely, nevertheless, because of possible doubt, the non-committal term, *Early Pleistocene*, seems preferable.

PLATE III

Figures 61–86 from Moorhead (station 2)

- FIG. 61. *Equisetum arvense*. Piece of stem at node × 12.
- FIG. 62. *Sagittaria cuneata*. Achene × 8.
- FIG. 63. *Potamogeton zosteriformis*. Fruit (endocarp) × 6.
- FIG. 64. *P. foliosus*. Fruit (endocarp) × 7.
- FIG. 65. *P. Richardsonii*. Fruit (endocarp) × 7.
- FIG. 66. *Eleocharis intermedia*. Achene × 7.
- FIG. 67. *E. palustris*. Achene × 13.
- FIG. 68. *Cyperus erythrorhizos*. Scale × 10.
- FIG. 69. *C. erythrorhizos*. Achene × 10.
- FIG. 70. *Scirpus validus*. Achene × 9.
- FIG. 71. *S. acutus*. Achene × 8.
- FIG. 72. *Carex disperma*. Achene × 8.
- FIG. 73. *C. Bebbii*. Achene × 10.
- FIG. 74. *C. sychnocephala*. Achene × 8.5.
- FIG. 75. *C. rostrata*. Achene × 11.5.
- FIG. 76. *Juncus canadensis*. Seed × 27.
- FIG. 77. *Chorispermum hyssopifolium*. Fruit × 7.
- FIG. 78. *Polygonum lapathifolium*. Achene, with attached perianth veins, × 10.
- FIG. 79. *P. amphibium*. Flower × 6.5.
- FIG. 80. *P. ramosissimum*. Achene × 13.
- FIG. 81. *Rumex persicarioides*. Fruit × 7.
- FIG. 82. *Ranunculus Purshii*. Achene × 11.
- FIG. 83. *Potentilla norvegica* var. *hirsuta*. Achene × 10.
- FIG. 84. *Vaccinium angustifolium*. Seed × 12.
- FIG. 85. *Hippurus vulgaris*. Fruit × 13.
- FIG. 86. *Bidens cernua*. Achene × 8.

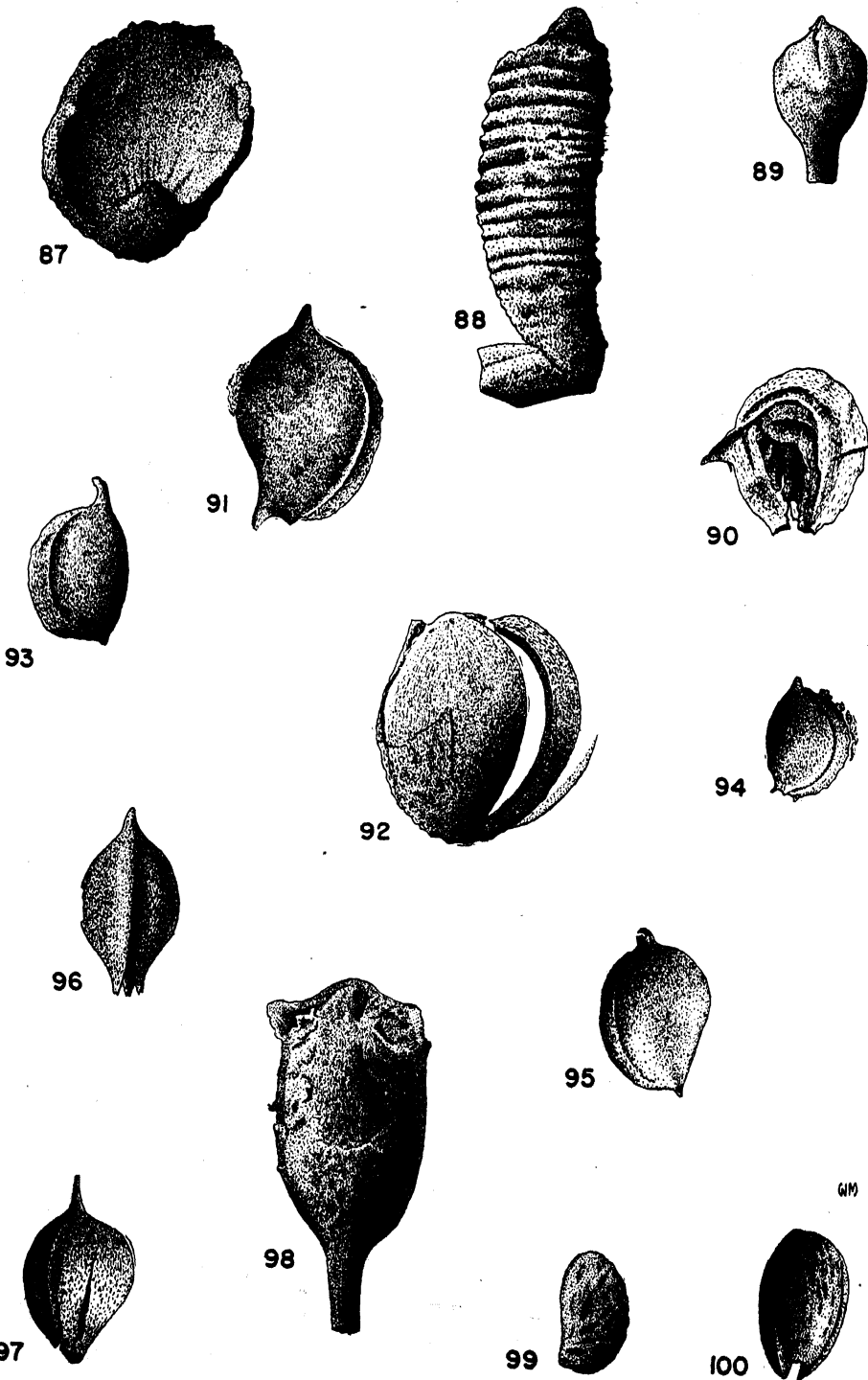


PLATE IV

Nebraskan till for it fits Leverett's ('32) statement that the "oldest drift consists mainly of a nearly black till in which a large amount of woody material still present in identifiable species was incorporated." All of the plant material recovered from this site is wood, occurring in the form of twigs, splinters, knots and fragments of roots. All of the pieces microscopically examined are spruce (*Picea*). The wood structure agrees more closely with white than black spruce, yet the possibility of a minor representation of the latter species is not excluded. As in the case of the wood from the Springfield station, some of the wood pieces are crusted with iron pyrite and cross sections often show a deposit of the mineral in the resin ducts and even in the tracheids.

Zumbrota, Station 9, Early Pleistocene (probable age 700,000–1,000,000 years).—The site is on U. S. Highway 52, about $1\frac{1}{4}$ miles south of Zumbrota. The bank on the west side of the cut is about 25 feet high while the one on the east side is nearly 10 feet lower. The upper $\frac{2}{3}$ of the till contains numerous boulders, some of which measure more than a foot in diameter. The wood-containing layer of blue-black till begins at a level of about 4 feet above the base of the cut and is exposed for a distance of approximately 100 feet. The till has the same color and texture as that of the

St. Charles cut. All the wood pieces have been identified as White Spruce (*Picea glauca*). The material shows a corresponding degree of aging and a similar iron-pyrite deposition to that of the St. Charles cut.

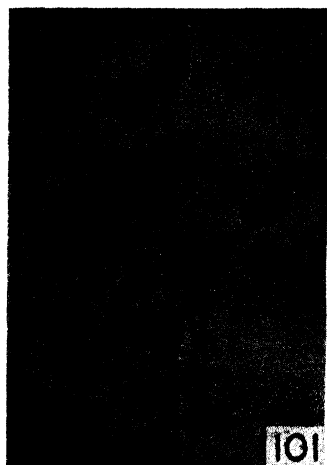
Pine Island, Station 10, Early Pleistocene (probable age 700,000–1,000,000 years).—The site, also on U. S. Highway 52, is located $1\frac{1}{2}$ miles north of the village. The cut is about 12 feet deep and only about 2 feet of the blue-black till is exposed. The till has the same color and structure as that of the two preceding stations and obviously belongs to the same drift sheet. The woody material is less abundant and not as well preserved as that obtained from the other two cuts. However, it was found to be in identifiable condition and all of it is White Spruce (*Picea glauca*).

Mankato, Station 13, Early Pleistocene (probable age 700,000–1,000,000 years).—The site is a deep road cut on Old Highway 7, $1\frac{1}{2}$ miles west of the city. The till in which the plant material occurs is not as dark as that of the St. Charles and Zumbrota sites, but nevertheless is most likely Nebraskan. It is indurated, contains a limited amount of small boulders and is overlain by a massive deposit of more bouldery buff-colored drift. Many pieces of wood were obtained from this place, some of which measured over a foot in length and 2–3

PLATE IV

Figures 87 to 100 (except fig. 88) are of plants from the Jackson well (station 20)

- FIG. 87. *Larix laricina*. Cone scale $\times 7.5$.
- FIG. 88. *L. laricina*. Short shoot $\times 6$ (from Springfield).
- FIG. 89. *Sparganium minimum*. Fruit $\times 10$.
- FIG. 90. *Sagittaria latifolia*. Achene $\times 7.5$.
- FIG. 91. *Potamogeton amplifolius*. Fruit (endocarp) $\times 7.5$.
- FIG. 92. *P. praelongus*. Fruit (endocarp) $\times 7.5$.
- FIG. 93. *P. Friesii*. Fruit (endocarp) $\times 7.5$.
- FIG. 94. *P. foliosus* var. *macellus*. Fruit (endocarp) $\times 7.5$.
- FIG. 95. *P. pusillus*. Fruit (endocarp) $\times 10$.
- FIG. 96. *Carex trichocarpa*. Achene $\times 7.5$.
- FIG. 97. *C. vesicaria*. Achene $\times 7.5$.
- FIG. 98. *Ceratophyllum demersum*. Fruit $\times 7.5$.
- FIG. 99. *Rubus strigosus*. Stone $\times 7.5$.
- FIG. 100. *Viola nephrophylla*. Seed $\times 10$.



101



102



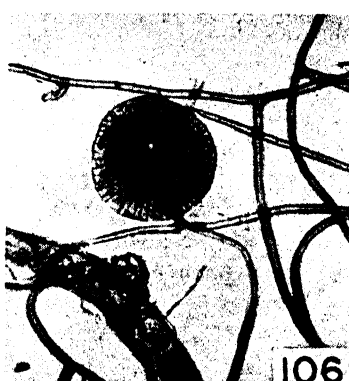
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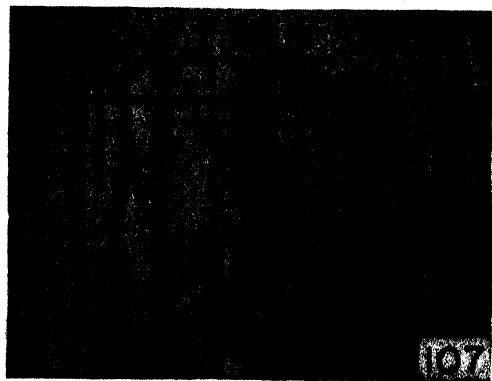
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105



106



107



108

PLATE V

inches in diameter. The wood is less deeply stained than that from the previously described stations and is practically free from deposits of iron pyrite. Noteworthy is also the fact that some pieces contain numerous fungal hyphae so well preserved that they stand out conspicuously in unstained microscopic sections (fig. 107). With the exception of one as yet unidentified Dicotyledon the wood is exclusively White Spruce (*Picea glauca*).

Garden City, Station 14, Early Pleistocene (probable age 700,000–1,000,000 years).—The site is a road cut on U. S. Highway 169, situated $\frac{1}{2}$ mile north of the village. It is approximately 18 feet deep with an exposure of nearly black till at the base of the east bank. In texture as well as color it is closely similar to the wood-bearing exposure of the cuts at St. Charles and Zumbrota and is evidently of the same age. In addition to wood, the layer contains innumerable pieces of lignite which indicate Cretaceous strata were incorporated into the drift. The very dark color of the deposit is likely due in part to the great amount of lignite in it. With the exception of a single piece of Butternut (*Juglans cinerea*) all the wood obtained from this site is spruce (*Picea*). There is a possibility that both white and black spruce are represented but the former unquestionably predominates.

St. Paul, Station 7, Early Pleistocene (probable age 700,000–1,000,000 years).—In the course of construction of the interceptor tunnels for the sewage disposal system of the Twin Cities during the middle 30's, a preglacial gorge was

encountered traversing part of the main business district of the city of St. Paul. The gorge is cut deeply into the Ordovician strata of sedimentary rocks underlying the city and is filled with glacial till. Underneath the site of the city market place several good-sized pieces of wood were recovered at a depth of 80 feet. The top drift of the locality is red Patrician but the till in which the wood was found is dark gray-green and in the vernacular of the excavators is spoken of as "greenpan." It is strongly indurated, contains numerous small quartz pebbles and occasional crumbly limestone pebbles. While the color of the till is not as dark as that of the stations in Winona and Goodhue counties which I have referred to the Nebraskan (see ante) I am nevertheless disposed to assign it to the same drift on the basis of texture and structure. The pieces of wood from this site, the largest of which measured 10 inches long and 4 inches in diameter, are very hard and heavy and exceptionally well preserved. Deposits of iron pyrite occur in the small cracks of the pieces and cross sections of them reveal the presence of the mineral in the resin ducts and tracheids. The wood is spruce (*Picea glauca*), one piece of which had the cell walls extraordinarily thickened.

In the following tabulation (table I) all the species¹⁰ recorded from the differ-

¹⁰ For the ferns and seed plants, the nomenclature is that of the 7th edition of Gray's Manual (1908) except for adopting in a few cases the changes in terminology effected by subsequent taxonomic treatments. The nomenclature for the mosses is mainly that of Grout's Moss Flora of North America (1928–40).

PLATE V

FIG. 101. *Rhizophogites Butleri*. Cluster of vesicles and hyphae $\times 50$. From Bronson well, station 1. FIG. 102. *Rhizophogites Butleri* $\times 91$. From Lake Agassiz silt of Moorhead deposit, station 2. FIGS. 103–4. *Rhizophogites minnesotensis*, showing hyphae and vesicles, $\times 91$. From an early Pleistocene deposit at Springfield, station 18. FIG. 105. *Trichothyrites pleistocaenica*. Cluster of perithecia with a tangle of hyphae of a Herpotrichia-like fungus $\times 97$. From an early Pleistocene deposit at Springfield, station 18. FIG. 106. The same, single perithecium more highly magnified $\times 225$. FIG. 107. Fungus hyphae in spruce (*Picea glauca*). From unstained section of wood $\times 220$. From early Pleistocene, Mankato, station 13. FIG. 108. *Mnium* sp. Part of leaf showing plastids in the cells $\times 220$. From Bronson well.

ent stations discussed in the preceding pages have been brought together. It has seemed desirable, also, to include in the table the species recorded by Cooper and Foote ('32) for the Minneapolis station and by Nielsen ('35) for the Rose Creek station in Mower County in order to

present as complete a summary as possible of all the Pleistocene plants at present known to have occurred in the state. It is deemed inadvisable to include any of the plants mentioned in the earlier reports on account of their only tentative identification.

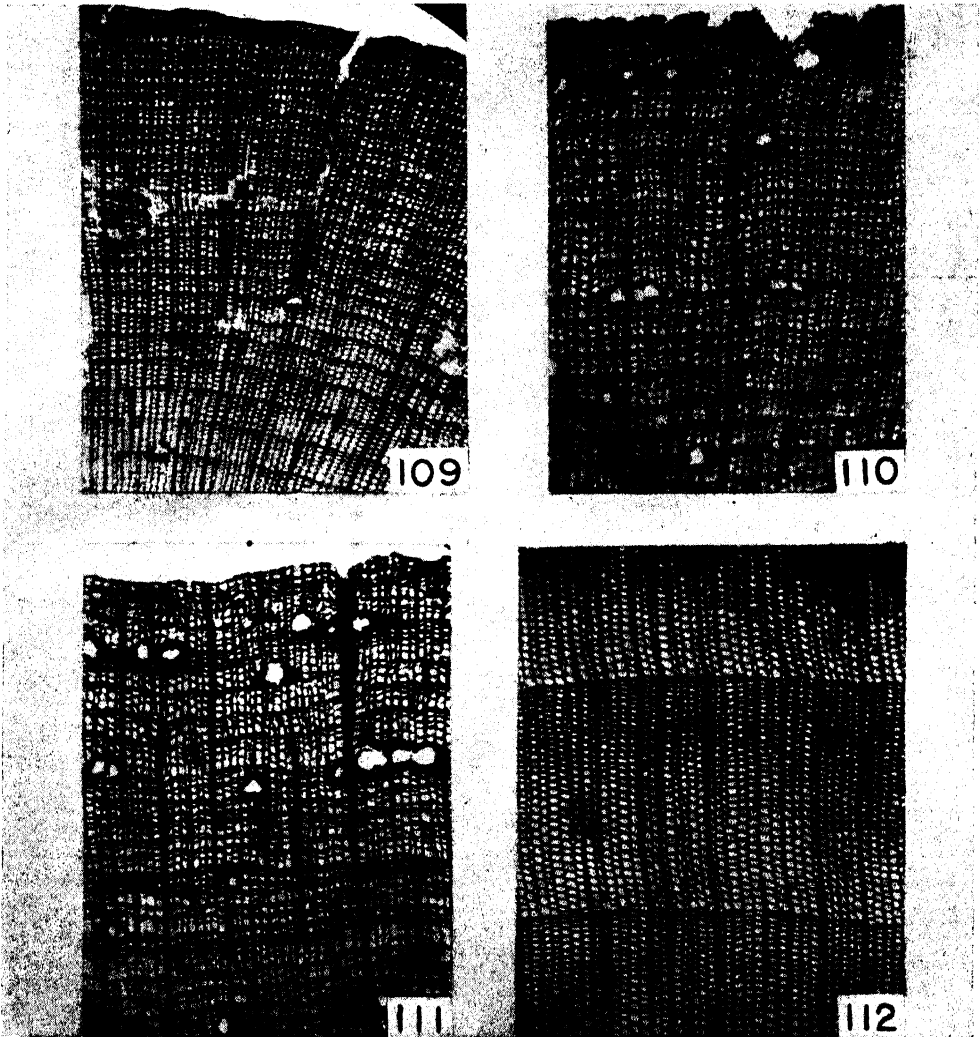


PLATE VI

FIGS. 109-110. *Picea glauca*. Sections of two different pieces of wood, showing progressive diminution in thickness of annual rings toward the periphery, $\times 50$. From Bronson well. FIG. 111. Section of another piece of White Spruce from the same well, showing four wider rings interpolated between two series of extremely narrow rings, $\times 50$. FIG. 112. *Picea glauca*. Section of wood from a stem 4 inches in diameter, showing normal growth and perfect preservation of cell structure, $\times 50$. From early Pleistocene at Springfield.

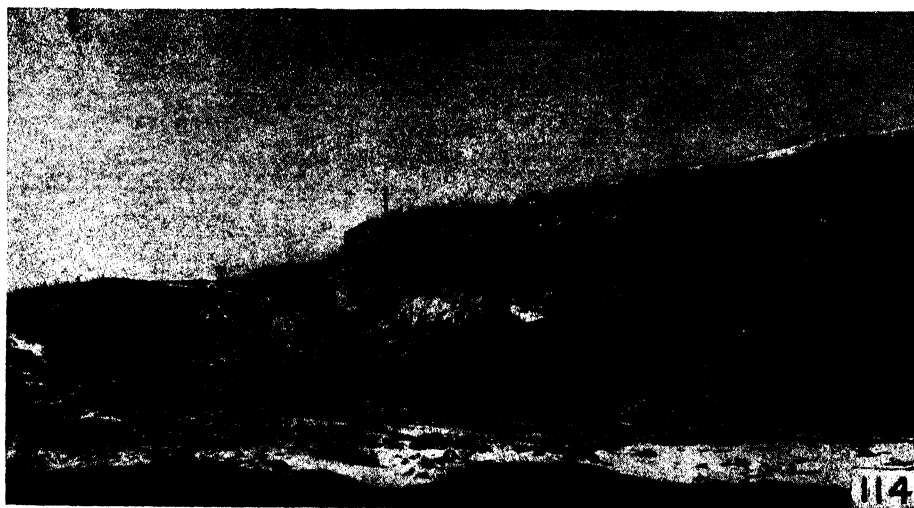


PLATE VII

FIG. 113. View of shale pit at Springfield, showing line of contact (a.b.c.) between Nebraskan till above and Cretaceous shale below. The till fills a pre-glacial gully eroded down to the base of the workable shale. FIG. 114. Another view of shale pit. The line of contact between till and shale is marked by the letters a, b, c, while the top of the Nebraskan till is outlined by d, e, f, and g. (Photos by C. W. Blue.)

CONCLUSIONS

A total of 126 entities, representing 68 genera and 38 families, are recorded in the foregoing table. Of this total 119 have been identified to species and varieties, 6 to genera and 1 to family only.

The list includes 3 species previously reported by Cooper and Foote ('32) from Minneapolis and 4 by Nielsen ('35) from Rose Creek, which have not been found in any of the other stations included in the survey. By far the greatest number of

TABLE I—Continued

[illegible]

TABLE I—Continued

[illegible]

species, as shown in the table, have come from the deposits at Bronson, Moorhead, Jackson and Springfield. So far as I have been able to ascertain, the first-named of these sites, with a total of 76 species, constitutes the second richest find of Pleistocene plants in America, being exceeded only by the remarkable deposits of the Don Beds near Toronto. The other three stations, with 39, 28 and 23 species respectively, rank fairly high among the many sites reported for interglacial plants in America.

Inspection of the table reveals that White Spruce (*Picea glauca*) was found in all but one of the stations. Six species occurred in four different stations, 9 species in three, and 32 in two. The remaining 78 species occurred singly among the 21 recorded stations. The well-nigh universal occurrence of white spruce, embracing sites which are referable to early as well as late Pleistocene, indicates that boreal climates prevailed over the region during parts at least of the different interglacial intervals. Supporting evidence for this assumption is found in the presence in some of the deposits of several species of arctic and boreal mosses such as *Distichium capillaceum*, *Camptothecium Woldenii*, *Campylium stellatum*, *Calliargon giganteum*, *C. turgescens*, *C. stramineum* and *Drepanocladus revolvens*. The great importance of fossil mosses as indicators of climatic conditions under which they live has been ably discussed by Steere ('42) and all of the above named species except the first are among those he reported for the Aftonian in Iowa.

A heavy preponderance of White Spruce in the Pleistocene forests of Minnesota is evidenced, not alone by its nearly universal occurrence but also by the great amount of spruce wood recovered from many of the sites, particularly the several road cuts of southeastern Minnesota, the early Pleistocene deposit at Springfield in the southwestern part of the state, and from the later deposits of the Moorhead and Bronson stations in the northwest. Wherever wood of other species has been

found, it is always in very minor quantity compared with spruce.

All the plants recorded are identified with living species except three fungi, viz. *Rhizophagites Butleri*, *R. minnesotensis* and *Trichothyrites pleistocaenica*, and the mosses *Neocalliergon integrifolium*, *Drepanocladus minnesotensis* and *Camptothecium Woldenii*, which are thought to be extinct. Aside from these I have not found anything that with long and painstaking study can not be matched with existing forms. It is true that the great majority of the species listed are from deposits of the last interglacial interval and the length of time involved is perhaps much too short to have effected any perceptible change or evolution. However, the plants found in the early Pleistocene deposits are equally referable to existing species. Obviously the present study is too limited in scope to shed much of any light on the evolution or extinction of plant species during the last glacial period. However, the assemblage of species here recorded seems to be sufficiently extensive and diverse to suggest that the local flora at least has come through the Pleistocene with very little change and very little loss.

SUMMARY

The early reports on interglacial plant deposits in Minnesota are briefly reviewed and the places from which they are recorded in the Final Report of the Geological and Natural History Survey of the state are shown on accompanying map. It is pointed out that the lack of specific identification of the materials renders these early records of little but historic importance except in so far as they reveal the wide-spread occurrence of interglacial plants in the Drift.

Interest in Pleistocene plants subsided as The Geological and Natural History Survey concentrated its work on the mineral resources of the state and it remained dormant until revived by the discovery of a rich Pleistocene deposit in Minneapolis in 1923.

During the last 15 years twenty additional sites for interglacial plant deposits have been discovered, consisting of road cuts, various kinds of excavations and deep wells.

The deposits range in age from early to late Pleistocene.

Five of the described sites have yielded 8 or more species each. Much the richest deposit occurred in the Bronson well, situated in the northwestern corner of the state, from which 76 species have been identified. With a few exceptions these are all members of the existing flora of the region, which suggests that a climate like the present one prevailed for some time during the Peorian interval.

The two richest deposits, viz. those of the Bronson and Moorhead sites, through the complete absence of remains of tundra plants furnish no evidence of the occurrence of tundra belts during either the advance or the retreat of the continental ice sheet during the last glaciation.

The number of plants identified and recorded from all the sites total 126. Their distribution among the different stations is shown by a tabular summary.

White Spruce was found in all but one of the stations and the bulk of woody material recovered in all cases is of this species. It is assumed that there was a heavy preponderance of White Spruce in the Pleistocene forests of the region.

All the species listed are identified with living forms except three species of fungi and three of mosses which appear to be extinct.

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A COMPARISON OF TWO ANTS OF THE GENUS *FORMICA*

MARY TALBOT

Lindenwood College, St. Charles, Missouri

This paper is a population study of two ants of the genus *Formica* and the species *pallidefulva*. Ants are often classified into many subspecies and varieties because differences between closely related groups are sometimes so slight that the taxonomists hesitate to distinguish them as true species. The *Formica pallidefulva* complex is such a group. Wheeler ('13) lists seven subspecies and varieties of the genus, which range in color from the pale yellow of the typical *F. pallidefulva* Latreille to the dark brown of *F. pallidefulva nitidiventris* var. *fuscata* Emery. I have encountered four of the *pallidefulva* group while collecting in the North Central states. Of these, *F. pallidefulva schaufussi* Mayr is the lightest and can live in the most exposed places, such as the poplar dunes of lower Lake Michigan. *F. pallidefulva nitidiventris* var. *fuscata* Emery, the darkest of the group, is more likely to be found in shaded woods. The two intermediate forms, which are treated in this paper, *F. pallidefulva schaufussi* var. *incerta* Emery and *F. pallidefulva nitidiventris* Emery, are the common *pallidefulvas*, being abundant and widespread in woods on sand or clay, in pastures, or along roadsides. These latter two ants are separated in Wheeler's key ('13) by the fact that *F. pallidefulva schaufussi incerta* workers have a few hairs on gula and petiolar border while *F. pallidefulva nitidiventris* do not. In general, *incerta* workers are a little lighter and less shining than are *nitidiventris*; but individuals vary so much from colony to colony or even within a colony that it is hard to decide whether a certain ant or colony belongs to one group or the other.

F. pallidefulva schaufussi incerta and *F. pallidefulva nitidiventris* were chosen for study with a two-fold purpose: to increase a series of studies in populations

of ants such as those carried out for *Prenolepis imparis* Say (Talbot, '43) and *Myrmica schencki* ssp. *emeryana* Forel (Talbot, '45a), and to try to find differences, other than structural ones, which would help to distinguish the two groups of ants. For such a study it was necessary to discover a habitat where both ants nested near each other, where both were subjected to similar changes of temperature, moisture, and light, and where both foraged for the same type of food. Such a location was found at the Michigan Biological Station near Cheboygan, Michigan. Colonies were abundant on the south slope of a sand ridge where aspens (*Populus grandidentata* Michx. and *P. tremuloides* Michx.) mixed with red and jack pines (*Pinus resinosa* Art. and *P. banksiana* Lamb), and the ground cover consisted mainly of bracken fern (*Pteris aquilina* L.) sumac (*Rhus glabra borealis* Britton), blueberry (*Vaccinium pennsylvanicum* Lam.), and reindeer moss (*Cladonia rangiferina* Web.). Here, during the summer of 1945, nests were dug to reveal their structure; colonies were collected and counted to determine population size and rate of development of brood; and observations were made on flight activities. During July of 1947, another series of colonies were dug in order to increase the number of records.

Nest structure.—Emerson ('38), in his study of termite nests, stresses the fact that "nest structures are morphological expressions of behavior patterns." With this in mind, similarities and differences in nests of *incerta* and *nitidiventris* were noted carefully to see if behavior differences between the two groups could be detected. In general, the nests were quite similar. Both ants are of the type which excavate the soil to form one or more vertical galleries from which radiate the

chambers where the ants live. The colonies studied nested in sand which, though gray and loose at the surface, was yellow and moist and firmly packed beneath. It was easy for the ants to excavate and held its shape about the chambers. The nest entrance was simply a hole in the sand. At times of major excavations, when nests were being dug or enlarged, a semi-circle of loose sand would be thrown up about it but never was there any structure resembling a crater or mound. These nest entrances, although fairly large ($\frac{1}{4}$ to 1 inch in diameter), were not conspicuous and were discovered by watching ants enter them. (Wandering ants will carry cake crumbs straight to the nest.) Entrances were usually in the open sand, but sometimes they would be under a bit of charred wood or log lying loosely on the sand. Occasionally there would be a second entrance 2 to 14 inches away from the main one. *Nitidiventris* nests seemed to have more of a tendency toward double openings than did *incerta*; about $\frac{1}{4}$ of *nitidiventris* had double entrance, but only $\frac{1}{6}$ of *incerta*.

Incerta and *nitidiventris* nests were similar in size of galleries and chambers. Galleries were $\frac{1}{4}$ to $\frac{3}{8}$ inches in diameter. Chambers varied in size and shape, typical ones being $1\frac{1}{2}$ inches long, 1 inch wide, and $\frac{1}{2}$ inch high with flat floor and domed roof. Differences were of two kinds: size of nest and its shape. Size differences concerned depth, number of chambers, and number of galleries. In general, *incerta* nests extended deeper into the sand. They averaged 28 inches, the deepest being 42 inches and the shallowest 22 inches. In contrast, *nitidiventris* nests averaged 18 inches in depth, the deepest being 24 inches and the shallowest 7 inches. The number of chambers differed, averaging 30 for *incerta* and 18 for *nitidiventris*. The number of perpendicular galleries was also greater in *incerta*, with 2.9 per nest in contrast to 1.7 per nest of *nitidiventris*. This larger size of *incerta* nests may be correlated with the fact that the colonies dug were found to

be larger. However a second contrast in nest structure does not have anything to do with size, and seems to be distinctly an expression of behavior difference. This concerns the shape of the nest. (See figs. 1 and 2.) *Nitidiventris* nests tended to spread out near the surface before narrowing to extend down, while *incerta* nests had no such surface expansion. Usually a *nitidiventris* nest had one gallery which ran horizontally for from 3 to 25 inches. Along this gallery might be a number of chambers almost touching the surface of the ground, or there might be a series of short galleries extending down for 2 to 6 inches from which chambers projected. Sometimes there would be one or two additional horizontal galleries beneath the first, all connected with runways and chambers making a sort of labyrinth in the first 2 to 6 inches. Beneath this the nest narrowed, being formed by 1, 2, 3, or rarely 4 galleries, going down into the sand independently (that is, not connected with each other) from which chambers radiated. *Incerta* nests did not show this wide spread of surface runways, but narrowed more quickly to the main perpendicular galleries. The simplest *incerta* nests had one chamber near the surface just beneath the entrance from which extended a perpendicular gallery with radiating chambers. More complex nests had several surface chambers or anastomosing galleries from which dropped 2, 3, or 4, or even 5 perpendicular galleries. These differences in nest structure were not clear-cut for every nest dug; rather they represented tendencies which were quite distinct in some colonies and hardly recognizable in others.

Populations.—For a comparison of populations 24 colonies of *nitidiventris* and 24 colonies of *incerta* were dug during the summer seasons of 1945 and 1947. Digging was begun during the early morning when most of the workers were in the nest, for, in contrast to many ants which forage during the night, these tend to remain in the nest during darkness.

TABLE I. *Population data for Formica pallidefulva schaufussi var. incerta Emery*

| Date | Queen | Mature workers | Callow workers | Winged females | Males | Female pupae | Male pupae | Worker pupae | Worker larvae | Eggs | Total |
|---------|-------|----------------|----------------|----------------|-------|--------------|------------|--------------|---------------|------|-------|
| 6-29-45 | 0 | 689 | | | | | 185 | | 180 | 15 | 1069 |
| 7-5-45 | 1 | 779 | | | | | 110 | | 272 | 271 | 1433 |
| 7-7-45 | 1 | 222 | | | | 3 | 11 | 97 | 163 | 43 | 540 |
| 7-7-47 | 1 | 336 | | | | 11 | | 80 | 276 | 362 | 1066 |
| 7-9-47 | 12 | 621 | | | | | | 494 | 618 | 939 | 2684 |
| 7-10-45 | 1 | 1563 | | 11 | | 147 | | 442 | 652 | 561 | 3377 |
| 7-14-47 | 9 | 1016 | | | | | | 670 | 964 | 870 | 3529 |
| 7-16-47 | 1 | 2120 | | | | 68 | 2 | 500 | 427 | 311 | 3429 |
| 7-17-45 | 4 | 354 | 43 | | | | | 471 | 445 | 462 | 1779 |
| 7-18-45 | 5 | 511 | 89 | | | | | 776 | 783 | 855 | 3019 |
| 7-22-47 | 2 | 331 | 44 | | | | | 238 | 319 | 188 | 1122 |
| 7-22-47 | 16 | 1826 | 91 | 11 | | 30 | 23 | 1979 | 1640 | 1433 | 7049 |
| 7-24-45 | 12 | 2059 | 291 | 52 | 4 | | | 2298 | 988 | 573 | 6277 |
| 7-25-47 | 2 | 194 | 13 | 3 | | | | 119 | 133 | 139 | 603 |
| 7-26-47 | 3 | 300 | 129 | | | | | 345 | 375 | 221 | 1373 |
| 7-27-45 | 6 | 371 | 91 | | | | | 452 | 262 | 121 | 1303 |
| 7-28-45 | 11 | 716 | 110 | | | | | 511 | 682 | 581 | 2611 |
| 7-28-47 | 3 | 735 | 141 | 33 | 6 | | | 746 | 214 | 196 | 2074 |
| 7-29-47 | 3 | 391 | 157 | 27 | 5 | | | 385 | 239 | 192 | 1397 |
| 7-30-47 | 6 | 638 | 288 | | | | | 732 | 311 | 300 | 2275 |
| 7-31-47 | 7 | 505 | 104 | 31 | | | | 395 | 430 | 390 | 1862 |
| 8-1-45 | 1 | 299 | 76 | | | | | 400 | 170 | 66 | 1012 |
| 8-8-45 | 1 | 1136 | 203 | | | | | 1201 | 624 | 482 | 3647 |
| 8-10-45 | 12 | 839 | 99 | | | | | 458 | 331 | 178 | 1917 |

There seemed to be little difference in rate of development of brood for the two. Larvae were over-wintered, and these developed into the first workers of the season as well as all of the males and

females to be produced that year. When the study began (6-26-45), egg laying was well under way (it continued uninterrupted through the summer), and many over-wintered larvae had already

TABLE II. *Population data for Formica pallidefulva nitidiventris Emery*

| Date | Queen | Mature workers | Callow workers | Winged females | Males | Female pupae | Male pupae | Worker pupae | Worker larvae | Eggs | Total |
|---------|-------|----------------|----------------|----------------|-------|--------------|------------|--------------|---------------|------|-------|
| 6-26-45 | 1 | 183 | | | | 6 | | 128 | 35 | 25 | 378 |
| 6-27-45 | 1 | 786 | | | | 45 | | 43 | 176 | 118 | 1169 |
| 6-28-45 | 1 | 94 | 12 | | | | | 26 | 29 | 14 | 176 |
| 7-4-45 | 1 | 766 | | | | 109 | | 97 | 595 | 349 | 1917 |
| 7-8-47 | 1 | 650 | | | | 47 | 4 | 37 | 495 | 309 | 1543 |
| 7-11-45 | 1 | 1389 | | 7 | | 136 | | 259 | 697 | 459 | 2948 |
| 7-11-47 | 1 | 1008 | | | | 152 | | 240 | 361 | 285 | 2047 |
| 7-13-45 | 1 | 450 | | | | | 70 | 76 | 324 | 180 | 1101 |
| 7-15-47 | 1 | 901 | | 35 | | 41 | | 400 | 596 | 215 | 2189 |
| 7-16-45 | 1 | 702 | | | | | | 159 | 191 | 161 | 1649 |
| 7-18-47 | 1 | 799 | | | | | | 45 | 187 | 456 | 1596 |
| 7-19-47 | 1 | 1075 | | | | 141 | 1 | 345 | 684 | 463 | 2710 |
| 7-20-45 | 1 | 493 | | 7 | | 34 | 7 | 243 | 572 | 236 | 1593 |
| 7-20-45 | 1 | 282 | 89 | 38 | 1 | 5 | | 516 | 222 | 186 | 1350 |
| 7-24-47 | 1 | 493 | 73 | 42 | | | | 575 | 436 | 391 | 2009 |
| 7-25-47 | 1 | 334 | | | | | | 212 | 161 | 53 | 761 |
| 7-26-47 | 1 | 515 | 120 | 45 | 2 | | | 628 | 505 | 197 | 2013 |
| 7-27-45 | 1 | 400 | | | 1 | | | 172 | 306 | 91 | 1000 |
| 7-31-45 | 1 | 367 | 4 | 10 | 29 | | | 244 | 303 | 198 | 1156 |
| 8-1-47 | 1 | 842 | 155 | 99 | 4 | | | 510 | 488 | 346 | 2445 |
| 8-3-45 | 1 | 1667 | | 154 | | | | 785 | 717 | 377 | 3701 |
| 8-7-45 | 1 | 316 | 24 | | | | | 225 | 254 | 83 | 903 |
| 8-9-45 | 1 | 1139 | 219 | | | | | 538 | 539 | 143 | 2579 |
| 8-11-45 | 1 | 648 | 118 | | | | | 493 | 442 | 178 | 1880 |

developed into worker, male or female pupae. However, few pupae were ready to emerge as callow workers. Callows did not become abundant until the middle of July.

During the digging of *incerta* and *nitidiventris* populations one difference in brood became noticeable. This was the proportion of naked to covered pupae. Ants of the genus *Formica* usually have their pupae enclosed in silken cocoons, in contrast to the *Myrmecine* ants, whose pupae are naked. However, in almost any *Formica* colony there are some naked pupae. *Incerta* followed the general pattern of having a few naked pupae in almost every colony; but it was soon discovered that *nitidiventris* had the proportion of naked pupae considerably increased. Therefore records were kept of the ratio of naked to covered pupae and it was found that, while *incerta* had 89.54 per cent of its pupae covered with cocoons, *nitidiventris* had the proportion reversed with 77.40 per cent of its pupae naked. This difference was constant for the two years studied. In 1945 *incerta* had 87.47 per cent covered pupae while *nitidiventris* had 28.01 per cent covered. In 1947, 91.64 per cent of *incerta* were covered and only 15.44 per cent of *nitidiventris*. *Incerta* colonies were constant in that all of the colonies had more covered than naked pupae. Two colonies had no naked at all. *Nitidiventris* was not as constant; of the 24 colonies counted 7 approached the *incerta* condition of having fewer naked than covered. Two of this 7 had only covered pupae. In both ants there was a larger percentage of covered pupae early in the season before they became numerous in the colonies.

Flight.—Both *incerta* and *nitidiventris* produced their males and females from over-wintered larvae. These larvae had already pupated by the latter part of June, when digging began. The first winged females were found in nests on July 10 in 1945 and on July 15 in 1947, but emergence from the pupal stage varied greatly in different colonies and dragged

out until flight time. Males developed a little more slowly than females; some *nitidiventris* males were still in the pupal stage on July 27, 1945, one day before flight began for some colonies. Evidently some of the winged ants fly as soon as they are fully pigmented, though the first to emerge may have two or three weeks in the nest before flight.

Of 21 *incerta* colonies dug before flight time, 12 included winged ants or male and female pupae. Six of these 12 had both males and females, 2 only males, and 4 only females. Of 21 *nitidiventris* all but 2 colonies produced winged ants. Seven of the remaining 19 had both males and females, 8 had only females, and 4 only males. Mean female production of the 19 *nitidiventris* colonies was 60.7; mean male production was 18.5. The 12 *incerta* colonies showed a mean female production of 35.6 and mean male production of 28.8. However, observations at flight time gave the impression that there were many more females than males.

Flights are recorded for 1945 only. In 1947, observations ceased on August 1st, and at this time flight had not begun. For both species flight itself was unspectacular and long drawn out. *Incerta* flights were recorded for 10 days, July 15, 16, 17, 18, 19, 23, 24, 25, 26, 27. Days during this interval when flight did not occur (July 20, 21, 22) were dull with overcast sky. Temperatures on these mornings hovered around 68° F., which was probably high enough for flight had the sun been bright.

Incerta flights could be watched carefully because a group of fourteen nests lay quite close together. Of these, winged ants were seen at seven nests some time during the flight period. One nest had winged ants for only 1 day, three for 2 days, one for 5, and one for 6, and one for every flight day. All of these colonies produced females predominantly. For the 4 having the sparsest flights no males were seen at all.

Incerta flight activities were dull. Workers took no part in the flight, but

continued foraging; nest entrances were not modified in any way and never were winged ants numerous. A female would come to the edge of a nest entrance, stand there a few seconds, perhaps dart back out of sight, then come back, hesitate again, and climb out on to the sand. She might move back and forth across the sand, or she might climb the first thing reached, usually a bracken fern leaf or a nest-marking stake. At the top she would stand for a while, then vibrate her wings very rapidly and fly high into the air to the south where light was greatest. Sometimes a female would climb up and down several brackens before flying and sometimes she would run about on the sand for several minutes. Males looked and acted like wasps. One would walk over the sand waving his antennae slowly, then fly abruptly. The largest number of winged ants seen at a nest at one time was 5 and often there were minutes when none was in sight.

Only one copulation was seen. The female was standing on a stake; the male attached to her gaster was half upside down and supporting himself with hind legs and tips of wings. When they separated the female moved down to the ground and then directly into a near-by nest.

Incerta flights took place in the early morning when the sun was slanting across the plot, but exact time of flight varied from colony to colony and from day to day. Accurate timing was rather difficult since only by repeated observations could one be sure that the colony was in flight at all. The earliest that males and females were seen aboveground was at 5:45 A.M. (e.s.t.). At this time the temperature at the nest was 65° F. Next day, winged ants were not seen until 7:25 A.M., but the temperature was a little lower (60° F.). On the other days the first winged ants left the nest between 7:10 and 7:20 A.M. at temperatures between 60° and 66° F. One female was seen to fly at 6:10 A.M. (66° F.), others between 7:10 and 8:10 A.M. (64–71° F.). The latest any winged

ants were seen was at 9:00 A.M. (70° F.). On other days flight was over between 7:30 and 8:57 A.M. (70–71° F.). Since these ants are so sensitive to light it seems likely that intensity or slant of light may play a greater part in determining flight time than does temperature.

A flight from a female nest at Tiffin, Ohio, in 1943 (Talbot, '45b) took place at the same time of year but occurred about an hour later in the day and at temperatures 5 to 15 degrees higher. But here again flight occurred when the morning sun touched the nest.

Flight records for *nitidiventris* could not be so complete as those for *incerta* because nests were so widely scattered that no group could be kept in sight. Therefore flights were watched from two colonies, one producing nothing but females, and one exclusively male. Their flights followed the same general pattern as did those of *incerta*.

Females flew on July 28, 29, 30 and August 1 and 2, leaving the nest between 8:40 and 10:40 A.M. at temperatures of 71° to 87° F. Males had 4 days of flight—August 1, 2, 3, and 4—and flew a little earlier, from 8:10 to 8:37 A.M., at temperatures between 75° and 80° F. The fact that the two colonies did not have exactly the same flight days is not surprising since individual colonies of *incerta* varied considerably in their days of flight. *Nitidiventris* flights may be considered to cover at least the 7 days from July 28 to August 4.

These studies did not identify the external stimulus which might have affected initiation and cessation of flights. It is regretted that light intensity records could not be made since the *pallidiflava* ants seem to be greatly influenced by light in various ways and flights seemed to begin at about the time that the morning sun reached the nests. Temperature was not the ultimate deciding factor, and relative humidity appeared to have no discernible significance for this species.

Studies of ants such as these, which have sparse flights, bring out quite clearly

that flight is not as stereotyped an activity as is sometimes supposed, and show that a great variety of reaction may occur from colony to colony. If individual colonies are studied during the entire flight time, this same diversity of action can also be shown for ants which have conspicuous flights.

Colony founding.—*Lasius niger alienus* var. *americanus* Emery illustrates the common method of colony founding among ants. On a day of flight the female leaves the nest, is fertilized, breaks off her wings and crawls down away from the light. She excavates a small chamber in the earth and stays there until her first eggs are matured and laid. Even then she does not leave the nest but feeds the larvae on regurgitated food. Being ill fed, these first larvae become stunted workers. However, they take over the duties associated with the workers: dig out the chamber, forage for food, excavate a larger nest, and care for subsequent larvae.

Nitidiventris showed every evidence of conforming to this pattern. No very young colony was discovered. The smallest, with 106 workers, may have been several years old but was evidently not mature, for no males or females were produced. Each colony had one female only, evidently the one which had founded it. Nests were numerous but scattered over the sand slope (with no sign of clustering) as if they had been dug at the place where the female lighted after her nuptial flight, or had later been moved by the colony with no reference to any other colony. If a colony is founded by a single queen and grows gradually from year to year, then it might be expected that the nest size would increase with the growing colony. Similarity between size of colony and size of nest was not striking, but some little correlation could be seen. The 12 smaller colonies had nest depths ranging from 7 to 18 inches with a mean of 15, while the 7 larger colonies had nests ranging in depth from 18 to 24 inches with a mean of 20 inches. Chambers of

the first group ranged from 2 to 23, for the second from 15 to 41.

However, *incerta* showed some interesting variations in behavior which hinted at a different method of colony founding. No clear-cut story could be secured, but the following field observations bear on this subject.

1. During flight days one female was seen to mate and then immediately walk to and enter a near-by nest.

2. Of the 24 colonies dug, 16 had multiple dealate queens. One colony had 16, three had 12 each, and the average for the 24 colonies was 5.1 females per colony. This was in sharp contrast to *nitidiventris* which never had more than one queen to a colony.

3. Once workers were seen pulling a dealate queen across the sand.

4. One record was kept of what seemed to be a case of the "budding" of a colony:

June 23, 1945—Ants from nest 5 are carrying larvae, pupae and workers to a new opening 3 feet away. At this new entrance (now named nest 6) many ants are busy excavating, and there is a conspicuous circle of yellow sand about the opening.

June 25—Now ants are carrying larvae, pupae, and workers in both directions to the new nest and back from it to the old one.

July 6—About 4 feet from nest 6 there is now a new entrance (called nest 7), with a half circle of freshly excavated sand. When cake crumbs are scattered ants come out of the new nest and take them back to nest 6.

July 11—Ants from nest 7 still take crumbs to nest 6.

July 14 and 17—Workers are carrying pupae from nest 6 to nest 5.

July 24—Workers are carrying larvae and pupae from nest 7 to nest 6.

5. No very shallow nests were found. The smallest colony had a nest depth of 28 inches and the most shallow nest (belonging to the third smallest colony) was 22 inches deep. The 12 smaller colonies had nest depths ranging from 22 to 32

inches and averaging 24 inches. The 12 larger had their nests ranging in depth from 21 to 42 inches with a mean of 30 inches. The 42 inch deep nest (belonging to a medium sized colony) was much deeper than any other, the next deepest being 36 inches.

6. *Incerta* was not so common on the sand slope as was *nitidiventris*; yet a large group of colonies were found at one place.

These observations, scattered though they are, lead one to speculate that colony founding may be somewhat as follows: The female, after the mating flight, enters a colony of her own species and lives there for a time, together with any other females which may have entered. Then a group of workers leave the nest and excavate a new one near-by. They carry larvae and pupae with them and guide a queen to the new nest. For several days or weeks there is traffic back and forth, for in any moving activity some ants are apt to carry brood back to the home nest. Gradually the ties with the

old colony are broken and a new colony is established, complete with mature, full-sized workers, queen, and a well excavated nest. Ultimately there will grow up a group of such colonies. This theory may or may not be correct; further observations will be necessary before it can be substantiated or discarded.

This study has done little to clear up the taxonomic status of the two types of *pallidefulva*. I can separate workers of the two more quickly and with more assurance than when the work was begun but there are still workers which are anybody's guess. If a nest is spread out near the surface, has entrances and does not go deep it is almost certain to house a colony of *nitidiventris*, but some nests have a medium spread and a medium depth. If there are more naked than covered pupae in a colony it is *nitidiventris*, but if there are only a few it may be either. Perhaps a study in another part of the range of the two ants would reveal more clear-cut differences.

SUMMARY

Population studies were made of two closely related ants, *Formica pallidefulva schaufussi incerta* Emery and *Formica pallidefulva nitidiventris* Emery. The similarities and differences which were found are summarized below:

Formica pallidefulva schaufussi incerta

Nest structure:

Depth

Average—27.2 in. deep

Range—22 to 42 in.

Number of chambers

Average—30

Number of perpendicular galleries

Average—2.9

Number of entrances

$\frac{5}{6}$ th of the nests had only one entrance. When a second occurred it was usually near the first.

Nest spread near surface

Usually there was only a little spread of galleries or chambers near the surface.

Formica pallidefulva nitidiventris

Nest structure:

Depth

Average—17.7 in. deep

Range—7 to 24 in.

Number of chambers

Average—18

Number of perpendicular galleries

Average—1.7

Number of entrances

$\frac{1}{4}$ th of the nests had more than one entrance. They were from 2 to 14 inches apart.

Nest spread near surface

Usually a horizontal gallery with a series of chambers extended just under the surface for from 3 to 35 in.

Nests of *incerta* and *nitidiventris* were similar in their location, and in the size and structure of entrances, galleries, and chambers. The differences mentioned above would not necessarily hold for each individual nest dug, nor are they statistically significant.

Populations:

Colony size

Average population—2351.96
Range of populations—540 to 7049
Average no. of workers—855.00
Worker range—222 to 2350
Proportion of covered and naked pupae
87.47 per cent covered

Populations:

Colony size

Average population—1700.54
Range of population—176 to 3701
Average no. of workers—713.04
Worker range—106 to 1667
Proportion of covered and naked pupae
28.00 per cent covered.

Incerta and *nitidiventris* were similar in rate of development of brood. Over-wintered larvae developed into males, females, and the first workers of the season. These emerged as adults about the middle of July. Differences in size of colony vary so much within each species that the larger mean for *incerta* is not mathematically significant. Also the proportion of naked to covered pupae will not hold for each individual colony studied.

Flight:

Flight days (1945):

July 15, 16, 17, 18, 19, 23, 24, 25,
26, 27

Time of day of flight:

6:10–8:10 A.M.

Temperatures at flight time:

61°–71° F.

Flight:

Flight days (1945):

July 28, 29, 30, August 1, 2, 3, 4

Time of day of flight:

8:10–10:40 A.M.

Temperatures at flight time:

71°–87° F.

In each case there was a tendency for a colony to contain mostly females or mostly males. More females than males were produced. *Nitidiventris* lagged after *incerta* in date, time of day, and rising temperature. However, these differences cannot be taken too seriously since only two colonies of *nitidiventris* were studied and others may have varied from these. For both *incerta* and *nitidiventris* flights occurred at about the time that the morning sun slanted across the nests. Flight activities were similar.

Colony founding:

The theory is advanced that after flight the female may return to a colony of her own species and that later the colony may "bud" when workers from it excavate a new nest, guide a female to it, and stock it with larvae and pupae from the old colony. Thus a cluster of colonies may develop in one small area.

Colony founding:

No evidence of the "budding" type of colony founding was discovered.

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FOREST SEQUENCE AND CLIMATIC CHANGE IN NORTHEASTERN NORTH AMERICA SINCE EARLY WISCONSIN TIME¹

PAUL B. SEARS

Oberlin College

The classification of climates is still largely an empirical matter. Thornthwaite ('43) is quite explicit on this point, and both he and Köppen have used natural communities as the basis of reference in their systems. I am assuming therefore that the larger formations such as coniferous and deciduous forests are primary climatic indicators. I make the further assumption that consistent and clearly marked shifts of the major associations with a given formation are valid evidence of climate changes of secondary order. I am also assuming that climatic changes associated with the advance and retreat of continental glaciers have been of sufficient magnitude to affect peripheral biological communities.

The considerations of postglacial change must naturally start with conditions beyond the ice border at the phase of maximum extent of the Wisconsin ice-sheet. Trask, Phleger, and Stetson ('47) find that the most recent sediments of the Gulf of Mexico, with their appropriate warm water faunal remains, are widely underlain by a definitely subarctic faunal layer. Below this is a cool-water faunal sediment, and below that another subarctic layer. The two subarctic layers represent, in the opinion of those authors, a single major glacial epoch.

Fossil evidence of Canadian conifers has been found in Florida (Davis, '46), South

Carolina (Cain, '44), North Carolina (Buell, '46), Louisiana (Brown, '38), and Texas (Patzger and Tharp, '47). The age of this material is not in every instance known, but much of it is clearly Wisconsin, indicating an extensive climatic displacement beyond the ice front at that stage of the Pleistocene. Thus the record of both land and marine sediments adds a heavy burden of proof against any claim of glacial refuges for temperate vegetation within or very near to the Wisconsin glacial margin. Such vegetation was, however, present, along with northern conifers at the southern stations referred to.

It is, of course, possible that alpine conifers may have moved *northward* from Mexico into lower altitudes across the Rio Grande during periods of cold climate. If this did happen, it would complicate the record as now understood, but ought not to change its essential meaning.

North of extreme ice limits, the physiographic record of the retreating glaciers, so far as it is known, has recently been summarized on a detailed map by Flint and others ('45). This and Flint's new volume on the Pleistocene (Flint, '47) and that of Zeuner ('45), have been invaluable sources of reference.

Beginning with the Tazewell substage, the record in the area of this study is one of considerable retreats, followed by relatively slighter readvances. Thus the Cary, advancing after retreat of the Tazewell, overlapped somewhat the northern limits of the latter. In turn the Valders (Mankato?) did likewise with the Cary. After the Valders retreat which resulted in Lake Agassiz, there was a "conspicuous re-expansion" (Flint, '47). This formed what is now called Lake Campbell (Antevs, personal communication).

¹ Based upon a paper prepared for the Symposium on Bottom Sediments, a joint session of the Ecological and Limnological Societies of America, Chicago, December 31, 1948. Thanks are due to Professor Ira T. Wilson for suggesting this paper, to Professors L. R. Wilson, F. O. Grover, and R. F. Flint, D. B. Lawrence, W. S. Cooper, and to Dr. Ernst Antevs for comments which have substantially clarified my own ideas. This kindness should not involve them in any criticism which the paper may receive.

The subsequent course of the ice front is as yet imperfectly known. There appear, however, to have been two periods of oscillation. One was "in the region of Cochrane (S. of James Bay)" (Antevs, personal communication). The other has been called by Matthes ('43) the "Little Ice Age" (Alpine-Alaskan in table I of the present article) and is described by him as marked by "a moderate recrudescence of glacial conditions for several centuries past," with a final period of retreat beginning in the last century. Counting the Tazewell, then, there should be at least six episodes, each involving advance and retreat, to be reckoned with.

The climatic conditions favoring glacial advance are not as yet demonstrated, but cold and moisture are clearly requisite. On the other hand, ice will undergo conversion of state to liquid with rise in temperature, and to gas with increasing desiccation. Thus, either warmth or dryness could be effective in causing retreat, and their combination should certainly be so.

Admittedly the problem is complex and obscure, but for purposes of discussion it may be assumed that ice retreat is due to the shifting or expansion iceward of climates that are warm or dry or both. Presumably the impact of such a climate is most intense and prolonged in the direction from which the warm or dry air masses of the new climate come, briefest and weakest at the ice center. Conversely the effect of a glacial climate may be assumed to be most intense and prolonged at the center of ice accumulation and to diminish in intensity and duration away from the periphery of the ice.

Whether or not these assumptions make sense in terms of orthodox climatology, they serve the needs of the ecologist who has to deal with the record of mass movements of communities and of shifting vegetation regions. Such is the significance of Figure 1, in which Deevey ('39) indicates the trend of climatic favorability for deciduous forests at three stations at different latitudes.

The changes in postglacial vegetation as indicated by pollen profiles do not show a simple unvarying trend from their beginning to the present. Neither does the floristic evidence from the present distribution of communities. It has been difficult to establish generalizations from the profiles that have been obtained in northeastern North America. These profiles do have definite regional characteristics (Sears, '35a), and most of them show

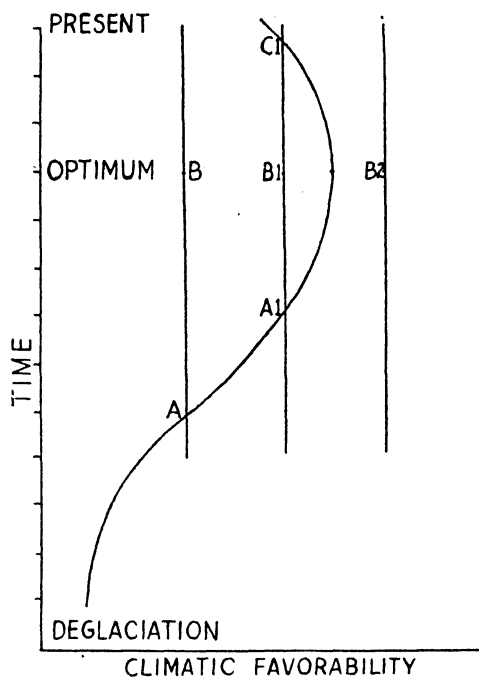


FIG. 1. Schematic curve, after Deevey ('39), to show relation of climatic favorability for deciduous forest to latitude. The three vertical lines represent three separate stations arranged from south (left) to north (right).

coniferous pollen at the base, clearly indicating glacial influence. Furthermore, the more northern profiles show a recent relative increase of, or return to, coniferous pollen.

In Ohio, Connecticut, and New Hampshire, near the Wisconsin margin, Sears ('42a), L. R. Wilson,² Deevey ('43), and

² Manuscript, dated 1947, entitled "Pollen analysis of the Amanda Peat, Licking Co., Ohio."

Krauss and Kent ('44) have reported evidence of at least five phases, as follows:

- V. Mesophytic Deciduous—Beech, Maple, Hemlock (at present)
- IV. Xerophytic Deciduous—Oak, Hickory
- III. Mesophytic Deciduous and Conifer—Hemlock, Beech
- II. Xerophytic Conifer—Pine
- I. Cold, Humid Conifer—Spruce, Fir

These phases are also shown from West Virginia, beyond the glacial border, by Darlington ('43), and the upper three from Syracuse, New York by McCulloch ('39), in a bog left by the lowering of Lake Iroquois. On the other hand, bogs from Indiana and southern Michigan show less regularity, and Tazewell bogs in Illinois studied by Voss ('37) show only the retreat of conifers and the advance of deciduous genera. Many of these last-named bogs are obviously truncated. To complicate matters, the bogs on Cary drift which Voss ('34) has studied in Illinois show substantially the same thing, except that the deciduous record is prolonged.

Farther north the agreement is better. From Minnesota and Western Ontario to New Brunswick and eastern Quebec, the sequence is spruce, pine, spruce, with a brief deciduous maximum frequently accompanying the pine (Wilson and Webster, '43). Thus, three clearly marked intervals obtain here, instead of the five found from Ohio eastward, or the equivocal conditions in Indiana, Illinois, and southern Michigan.

This situation has led to a marked divergence of explanations which have had a fair counterpart in Europe (Sears, '42c). Axel Blytt of Norway, on the basis of his studies of peat, proposed a series of postglacial periods as follows:

- f. Sub-Atlantic—cool, moist (at present)
- e. Sub-Boreal—warm, dry
- d. Atlantic—warm, moist

- c. Boreal—cool to warm, dry
- b. Pre-Boreal—cool, moist
- a. Sub-Arctic—cold

This theory assumes an alternation of wet and dry periods, with a warm maximum in the Sub-Boreal. Although subsequently modified it has been considered too rigid to fit the facts as developed in northern Europe. In its stead von Post of Sweden has suggested a more general hypothesis of rising temperature, followed by maximum warmth, and subsequent cooling with local variations. Yet the use of Blytt's terminology persists in many quarters. Added to the complexity is the question of contemporaneity in Europe and North America.

The 185 profiles upon which the present report is based represent the work of 29 different individuals. These reports differ greatly in techniques and in treatment of data. The greatest difficulty arises in studying those in which wind-pollinated herbs and various insect-pollinated species are reckoned in the same percentage system as the wind-pollinated upland forest dominants, instead of being tallied separately. For one source of confusion I must accept responsibility. Many workers have relied upon my pollen key of 1930 which does not include the pollen of *Picea canadensis*, which is larger than that of *P. mariana* (Potzger, '44). On the basis of measurement alone the former has often been mistaken for *Abies*. But the general climatic significance is not, fortunately, too different.

When Potter's study ('47) of 22 bogs in northeastern Ohio failed to show any consistent relations between profiles and successive moraine systems, it became clear that correlations would have to be sought on a larger scale. Such a scale is afforded by Flint's map ('45). So far as the pollen record is concerned, the key has been afforded by three documents. One is Wilson's (personal communication, see footnote 2) beautiful analysis of Amanda Bog in Licking County, Ohio, near the southern glacial margin. This is as yet un-

published, but has been most generously loaned to me. The second is a clean analysis of peat in the bed of former Lake Iroquois by McCulloch ('39). The third is Potter's ('47) own incidental location of Lakes Arkona and Whittlesey in the pollen column.

The basis for relating the various genera to glacial advance and retreat is as follows. *Picea* (and *Abies*) has in general a lower minimum temperature tolerance than *Pinus* (Hutchinson, '18). It has greater shade tolerance, and a higher moisture requirement. It is better suited, then, to the cold, humid climate assumed to favor glacial advance. Pine should not replace spruce in the normal course of plant succession. Where such replacement does occur on a large scale, we can only suggest the advent of a warmer, drier climate. To this statement there should be one exception. Spruce can thrive closer to the ice than pine. It should be the first in the wake of the retreating ice, but be replaced by pine as the ice becomes more remote, due to the continuing warm, dry climate which I have assumed to prevail during recession.

I have for these reasons used *Picea* as the general correlative of glacial advance, with the exception noted, and *Pinus* as the correlative of retreat.

Farther away from the ice, where deciduous forest is present, one would expect the effects of cold and moisture to be more diffuse. In general a moister, cooler climate should favor *Fagus*, *Acer*, and *Tsuga*. Similarly, a warmer, drier climate should throw the balance in favor of *Quercus* and *Carya*. And just as the proximity, even of a retreating glacier, should favor *Picea* rather than *Pinus*, the proximity of a warm, dry climatic region might exclude beech, maple, and hemlock, even at a time when climatic conditions in the vicinity of the ice might favor glacial readvance. This is a possible explanation of the comparative uniformity of Voss's ('34, '37) profiles in Illinois after the disappearance of conifers and the advent of deciduous forest. Since these

profiles lie well within the prairie peninsula, the Illinois region may have been more effectively cushioned against conditions which affected the later ice oscillations than was Ohio or—to use some of Voss's ('34) own data—northern Minnesota.

Again, at some of the more southerly stations in Indiana (Patzger and Wilson, '41) and occasionally elsewhere, there is evidence at the very top of the pollen record of a recent shift towards xerophytism. For example, beech may yield to oak and hickory. The meaning of this is by no means clear. Such a shift in vegetation is commonly associated with human exploitation. We have also had about a century of more or less general retreat of alpine glaciers in North America (Matthews, '43). Weather records appear to indicate a gradual rise of temperature during the same period, and by inference, a decrease in available moisture.

Summing up the existing information to be reconciled, we have the following:

Beginning with the Tazewell, there appear to be twelve alternating phases of climate, represented by six known advances and retreats of the ice. These are listed in table I. In the oldest continuous pollen profile available, that of Wilson (personal communication, see footnote 2) in southern Ohio, there appear to be, not twelve, but eight, alternating phases. There are thus four more phases of ice oscillation than there are vegetation phases to fit them on the basis of our assumptions.

Two of these four can be disposed of at once. The sedimentary pollen record could not begin inside the extreme Tazewell limits before the ice was out of the way. This leaves, on the basis of present knowledge, two ice movements without corresponding vegetation changes.

It is my judgment that the explanation of this discrepancy must be sought at the base of the pollen profiles, rather than at any higher level, although I am unable at the present time to arrive at any such explanation that takes into account Potter's ('47) data on Lakes Arkona and

Whittlesey. The trend towards slightly warmer (drier?) conditions in Phase 12, table I, is recent and faintly marked. The melting glaciers of Alaska have exposed spruce forest which had been covered by the advance just preceding. This spruce forest should be contemporaneous with the period of maximum warmth of Phase 10. That period was marked by the northernmost advance of deciduous trees, notably oak, and by the prevalence of oak-hickory and prairie in Ohio. The ecological evidence of this warm-dry maximum still persists. Such a climate must have been much more recent than the Agassiz-Campbell retreat, Phase 8. Furthermore, the earlier phases are so distinctly marked that any masking of their climatic effects on vegetation seems most improbable.

This brings us to the base of the pollen

profiles. The general absence of any evidence of tundra is a noteworthy feature, yet tundra has long been considered the normal vegetation between ice and coniferous forest. There can be no accumulation of forest pollen until (a) sedimentary basins are cleared of ice, (b) forests are near enough to these basins to contribute significant amounts of pollen, and (c) there is a proper balance between inorganic and organic sedimentation.

As regards (a) there is good evidence of the persistence of dead ice masses in northern Ohio. As to (b), the evidence already cited from southern United States suggests extensive displacement of vegetation during the Pleistocene. And with respect to (c), such preglacial lake sediments as I have examined show no significant amount of pollen, being mostly inorganic silt.

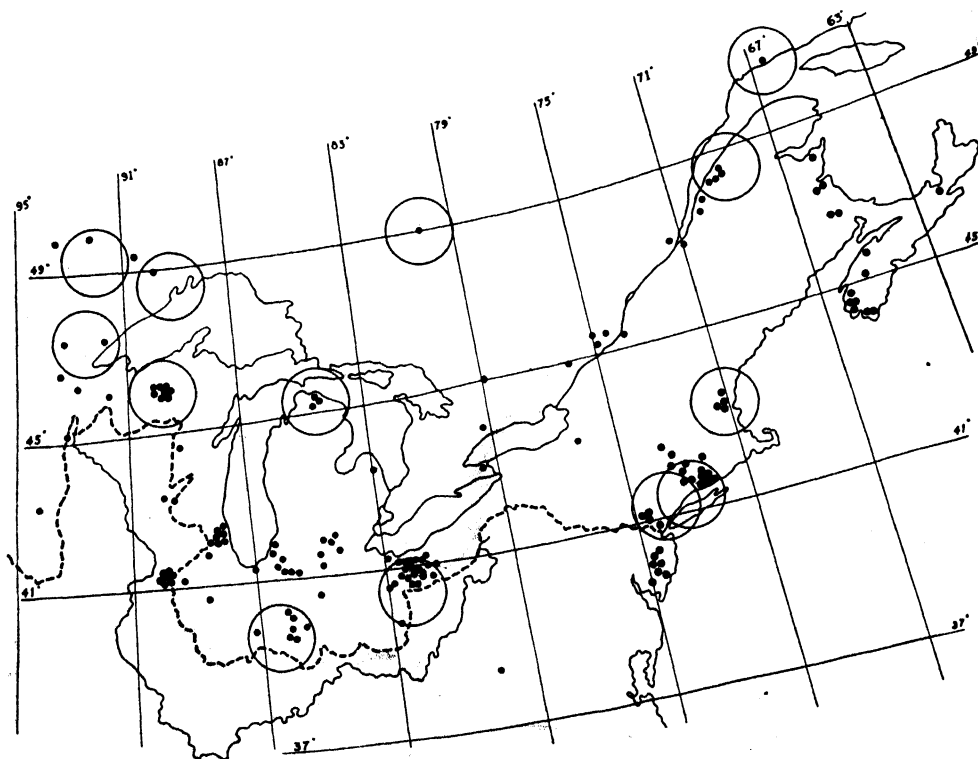


FIG. 2. Approximate locations of profiles studied. Larger circles enclose bogs whose oldest sediments show only northern conifers. Deciduous species, usually *Quercus*, present at inception of all bogs not circled.

TABLE I. *Suggested correlation of pollen profiles and Late Wisconsin substages*

| Glaciation | | Sequences of vegetation | | | | | | | |
|-----------------------------------|-------------|-------------------------|---------------|----------------|----------------|-------------|----------------|---------------|----------------|
| Subdivisions of Post-Mankato Time | Phases | Alaska | S. Canada | N. Michigan | N. Iowa | N. New York | N. Ohio, Conn. | S. Ohio | W. Va. |
| Alpine-Alaskan | 12. Retreat | Tundra | Pinus-Picea | Quercus-Betula | Subhumid Grass | Pinus-Tsuga | Quercus | Quercus | Quercus-Betula |
| | 11. Advance | Ice* | Picea-Pinus | Tsuga | Savanna | Fagus-Tsuga | Fagus | Tsuga | Fagus-Tsuga |
| Cochrane | 10. Retreat | Picea | Pinus-Quercus | Pinus-Quercus | Xeric Grass | Quercus | Quercus-Carya | Quercus-Carya | Quercus-Carya |
| | 9. Advance | ? | Picea | Picea | Forest | Picea-Tsuga | Tsuga | Pinus | Tsuga |
| Agassiz-Campbell | 8. Retreat | ? | ? | ? | ? | ? | Pinus-Quercus | Quercus | Pinus |
| | 7. Advance | ? | ? | ? | ? | ? | Picea | Picea | Picea |
| Subages | | | | | | | | | |
| Valders-Mankato | 6. Retreat | ? | Ice | ? | Ice | ?(4) | Pinus-Picea | Pinus | |
| | 5. Advance | ? | Ice | ? | Ice | ? | (3) Picea | Picea | |
| Cary | 4. Retreat | ? | Ice | Ice | Ice | Ice | (2) | ? | |
| | 3. Advance | ? | Ice | Ice | Ice | Ice | ?(1) | ? | |
| Tazewell | 2. Retreat | ? | Ice | Ice | Ice | Ice | Ice | Ice | |
| | 1. Advance | ? | Ice | Ice | Ice | Ice | Ice | Ice | |

Glacial Great Lakes: (1) Maumee, (2) Arkona, (3) Whittlesey, (4) Iroquois.

* Ice as used here refers throughout to that locally present at least in sedimentation basins.

For these reasons, I should say that the pollen record does not as a rule begin promptly with the ice retreat, but that, once begun, it reflects rather closely the subsequent climates that affect ice movement.

As a further general check, I have attempted to locate all pollen profiles from which the pollen of deciduous trees is absent at the base, that is, those from places in which the climate was, at the beginning of the record, too severe for anything but conifers. These appear to fall into two general lines (fig. 2). From Indiana east-

ward one line is made up of the oldest bogs. The second line consists of the youngest bogs studied, from northern Minnesota eastward and northward. In the oldest bogs to the westward, oak is present from the beginning, due presumably to the influence of the adjoining southwestern warm, dry climatic region. The inception of bogs of intermediate age must have taken place during a relatively warm general climate, for oak is present at the base in all of them. By this time deciduous forms had moved northward along the Atlantic coast (Sears, '42b), to

be represented in the earliest bog sediments of Nova Scotia and the upper St. Lawrence Valley (Auer, '30). But the period of greatest warmth seems not to have been in mid-postglacial time. Rather it was during Phase 10, when deciduous forms reached their farthest northward extension.

The correlation suggested in table I is based upon all of the foregoing considerations. Whether right or wrong in its essential features, it is at least explicit and should, for that reason, serve as a basis for future investigation and criticism.

SUMMARY

Beginning with the Tazewell Glaciation and including the present, there appear to be twelve known alternations of advance and retreat of the Late Wisconsin ice. These represent three recognized subages and three subsequent "episodes."

Comparison of 185 pollen profiles from northeastern North America indicates a regular alternation of humid and dry conditions, relatively speaking. The oldest continuous profile exhibits eight such alternations, or four phases fewer than those of the ice. Two of these can be accounted for by the presence of ice. The remaining two are assumed to belong to the transition from ice to forest, marked by dead ice, and some non-forest vegetation type whose pollen is insect-borne or does not preserve well, possibly a tundra-like seral stage and willow-alder shrub thicket. There is no evidence of any true tundra belt having existed.

Bogs along the southern glacial limits, and again along a line north of the great lakes, show no deciduous pollen at the base. This suggests two roughly parallel "cold lines" during the course of general retreat, with a milder period between.

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THE ECOLOGICAL SUCCESSION OF SPIDERS OF THE CHICAGO AREA DUNES

D. C. LOWRIE

New Mexico Highlands University

The ecological succession of spiders has been studied only incidentally by other workers. Elliott ('30) has treated the spiders of an Ohio beech-maple forest. Adams ('15), Sanders and Shelford ('22), Blake ('26), and Weese ('24) have concerned themselves with prairie, pine, and elm-maple animals, working little with the spiders. Park ('30), Strohecker ('37b), and Talbot ('34), working with coleoptera, orthoptera and ants respectively, have analyzed the distribution of these groups to find that it agrees in many respects with the plant succession. Strohecker concludes that "the change in typical species of orthoptera from foredune to pine associes is dependent upon decreasing soil moisture." Sunlight intensity, soil moisture, and soil temperature of a moderate, constant degree seem to be the main factors in the distribution of orthoptera in the dunes. Shelford ('13) mentions several species of spiders and, as this study will show, found some of the main characteristic species of the succession.

Collecting and field observation, carried on irregularly from 1935 to 1942, have demonstrated an ecological succession of spiders which corresponds to the plant succession with very few exceptions.

COLLECTING AREAS

Fryxell ('27) gives a general account of the Chicago area. Cowles ('99, '01) treats the Indiana-Michigan dune areas in particular. These unique areas are situated along the south and east shores of Lake Michigan where sand, deposited by the water from the eroding west shores, is piled up by the wind to form dunes which, in places, reach a height of nearly 200 feet. Sand-binding grasses begin the succession which continues through consecutive stages to the climax forest.

In addition to the collecting in this area, the black oak and foredunes of Waukegan, the black oak dunes of Kankakee and the climax forests of Saugatuck, Lakeside, and Warren's Woods in Michigan, and Smith, Indiana were investigated. Material from Waukegan and Kankakee are included because they are areas which have associations like those found in the Indiana area. However, in much of the discussion, species from these areas are not included, as other features such as the sparser population of Kankakee and the smaller area and more northern location of Waukegan (Lowrie, '42) change the association complex in several ways.

No regular plan of visiting the various areas was followed, as this study was not the primary object of the trips. One hundred eleven trips were made to the areas mentioned. Sixty-eight of these were made to the black oak dunes of Waukegan, Dune Acres, and Kankakee. As a result, the black oak dunes were the most thoroughly studied, the climax forest much less thoroughly and the other associes the least thoroughly studied. However, the material collected shows that certain species were present and therefore the report is valuable to that extent, although more collecting would show more species to be widespread. General observations of uncollected material helps to strengthen some points. The material, therefore, although incomplete in many respects, presents some facts which are well enough substantiated to be worthy of presentation. An additional factor influencing the writers decision to publish this material rather than waiting for more collecting before printing is the fact that he does not anticipate being able to collect further in this area.

Besides general collecting, a prelimi-

nary quantitative sweeping analysis of the herbaceous stratum was made. This analysis substantiates many of the observations of general collecting.

Data based on the collecting by Elliott in Lewis Woods, near Richmond, Wayne County, Indiana is included in table I and elsewhere. Though this area is nearly two hundred miles from the area studied, it is a beech-maple woods typical of this area and is therefore included though some of its species are undoubtedly more southern in affinities and would not be found in the Lake Michigan Dunes areas, and some species are lacking because of their more northern distribution.

THE DUNE ASSOCIES AND THE SPIDERS FOUND

The associes as discussed here are those of Cowles ('01).

THE BEACH: This incipient stage is entirely lacking in plants of any considerable bulk or height, so that virtually all web-building species are prohibited from permanent residence here. *Crustulina guttata* is found here and some of the species of micryphantids are probably beach residents, as they are all small spiders requiring very little substratum for web building. *Eustala anastera* and *Tetragnatha laboriosa* are occasionally found on the beach among the drift material but are not the usual members of the associes. Nine species of lycosids and two gnaphosids were collected on the beach, most of them having been found at night. Probably many of these species invade the beach from associes farther inland, as is the case with at least one other animal species, the toad, *Bufo fowleri*, which comes down to the lake at night to feed on spiders and insects and to wet itself in the water. It is likely that *Pardosa milvina*, *Pirata febriculosa* and *Schizocosa avida* are fairly regular inhabitants of the beach, as they have been found during the day beneath boards. *Arctosa littoralis* may certainly be placed in this associes, as it is found only on the beach where it hides during the day and

hunts during the night, feeding on insects in the drift line. Its presence at Kanakee may be explained by the fact that it has been found on the shores of lakes and rivers (Gertsch, '34). The Kankakee River marshlands once covered the region, probably leaving the spiders well established when the marshes were drained. As far as the spiders are concerned, this associes might well be named the lycosid associes or, more specifically, the *Arctosa littoralis* associes. The free-running habits of these spiders make it possible for them to utilize advantageously the beach as a night feeding ground. During the day, only accidental wanderers are likely to be active on the beach, most species seeking safety in the shade of the beach debris.

THE FOREDUNE: This associes consists of dunes up to fifteen feet in height which are formed by the binding action of two species of grasses, *Ammophila arenaria* (Linnaeus) Link and *Calamovilfa longifolia* (Hooker) Hackel, and the sand cherry *Prunus pumila* Linnaeus. These plants serve as a substratum for the webs of *Eustala anastera*, immature *Neoscona arabesca*, *Tetragnatha laboriosa*, *Crustulina guttata*, and *Dictyna bastoniensis* all small or medium sized spiders which can build their webs on the slight support the grasses offer. Of these five species, *Dictyna bastoniensis* was found to be most characteristic (table I), *Crustulina guttata* was rarely found and the other species were widespread. The species and individuals of lycosids are slightly less well represented; probably because there is less cover for them to hide under during the day. *Geolycosa wrightii*, which is found to some extent on the beach as well as farther back in the cottonwoods and open blowouts of any later stages, is one of the characteristic species of the foredune. Although the burrow openings may be closed during the day, they may be found dotting the landscape of the foredune and cottonwood dune at night. *Philodromus alascensis* is another spider common on the foredune. It is probably

TABLE I. Check list of the spiders of the dune associes

The presence of any species in an area is indicated by the following letters:

A—Warren's Woods, Michigan
 D—Dune Acres, Indiana
 K—Kankakee Co., Pembroke Twp., Ill.
 L—Lakeside, Michigan
 M—Miller, Indiana
 O—Ogden Dunes, Indiana
 S—Smith, Indiana
 U—Saugatuck, Michigan
 W—Waukegan Flats, Ill.
 X—Lewis Woods, Richmond, Ind.

The associes are indicated in the following manner:

B—Beach
 F—Foredune
 C—Cottonwood
 P—Pine
 O—Black Oak
 S—Subclimax
 B-M—Beech-Maple Climax

| Species | B | F | C | P | O | S | B-M |
|---|---|----|----|---|-----|----|------|
| Agelenidae | | | | | | | |
| 1. <i>Agelenopsis pennsylvanica</i> C. L. Koch | | | | | DK | | SX |
| 2. <i>Agelenopsis potteri</i> Blackwall | | | | | W | | |
| 3. <i>Agelenopsis ulahana</i> Chamberlin & Ivie | | | | | | O | ASU |
| 4. <i>Cicurina brevis</i> Emerton | | | | | D | | ASX |
| 5. <i>Cicurina pallida</i> Keyserling | | | | | | | ASX |
| 6. <i>Cicurina robusta</i> Simon | | | | | | | A |
| 7. <i>Coras juvenilis</i> Keyserling | | | | | | L | AS |
| 8. <i>Coras lamellosus</i> Keyserling | | | | O | | O | S |
| 9. <i>Wadolea calcaratus</i> Keyserling | | | | | | | AS |
| Anyphaenidae | | | | | | | |
| 10. <i>Anyphaena celer</i> Hentz | | | | | | O | AS |
| 11. <i>Anyphaena pectorosa</i> L. Koch | | | | | | L | ASX |
| 12. <i>Ayscha gracilis</i> Hentz | | | | O | DK | L | AS |
| Argiopidae | | | | | | | |
| 13. <i>Acanthepeira stellata</i> Walckenaer | | WD | | | WDK | | SX |
| 14. <i>Aranea angulata</i> Linnaeus | | | | | | | S |
| 15. <i>Aranea displicata</i> Hentz | | | | | WDK | | |
| 16. <i>Aranea foliata</i> Fourcroy | | | | | D | | |
| 17. <i>Aranea miniata</i> Walckenaer | | | | | | O | S |
| 18. <i>Aranea raji</i> Scopoli | | | | | DK | | SX |
| 19. <i>Aranea thaddeus</i> Hentz | | | | | D | | S |
| 20. <i>Aranea trifolium</i> Hentz | | | | | WDK | | S |
| 21. <i>Argiope aurantia</i> Lucas | | D | | | WDK | | |
| 22. <i>Argiope trifasciata</i> Forskal | | | | | WDK | | |
| 23. <i>Cyclosa conica</i> Pallas | | | | | | | AU |
| 24. <i>Cyclosa turbinata</i> Walckenaer | | | | | D | | |
| 25. <i>Eustala anastera</i> Walckenaer | M | WD | MO | O | WDK | O | SX |
| 26. <i>Larinia borealis</i> Banks | | | | O | WK | | |
| 27. <i>Leucauge venusta</i> Walckenaer | | | | O | DK | O | ASX |
| 28. <i>Mangora gibberosa</i> Hentz | | | | O | DK | | SX |
| 29. <i>Mangora maculata</i> Keyserling | | | | | K | O | SDA |
| 30. <i>Melepeira labyrinthica</i> Hentz | | | | | K | | S |
| 31. <i>Micrathena sagittata</i> Walckenaer | | | | | D | O | SDX |
| 32. <i>Neoscona arabesca</i> Walckenaer | | WD | O | O | WDK | | ASUX |
| 33. <i>Neoscona benjamina</i> Walckenaer | | | | | DK | | S |
| 34. <i>Neoscona pratensis</i> Hentz | | | | | DK | | |
| 35. <i>Pachygnatha xanthostoma</i> C. L. Koch | | | | | W | | |
| 36. <i>Singa pratensis</i> Emerton | | | | | K | | A |
| 37. <i>Tetragnatha elongata</i> Walckenaer | | | | | K | | U |
| 38. <i>Tetragnatha exensa</i> Linnaeus | | | | | W | | SX |
| 39. <i>Tetragnatha laboriosa</i> Hentz | | | | | WDK | | |
| 40. <i>Tetragnatha lacerta</i> Walckenaer | | | | | W | | |
| 41. <i>Tetragnatha pallescens</i> F. O. P.—Cambridge | | | | | WD | | |
| 42. <i>Tetragnatha straminea</i> Emerton | | | | | WD | | S |
| 43. <i>Theridiosoma radiosum</i> McCook | | | | | | | AS |
| Atypidae | | | | | | | |
| 44. <i>Atypus milberti</i> Walckenaer | | | | | | L | |
| Ciniflonidae | | | | | | | |
| 45. <i>Ciniflo bennetti</i> Blackwall | | | | | | | ASX |
| 46. <i>Tilanoeca americana</i> Emerton | | | | | WDK | L | X |
| Clubionidae | | | | | | | |
| 47. <i>Agroeca minuta</i> Banks | | | | | | O | |
| 48. <i>Agroeca ornata</i> Banks | | | | | | | A |
| 49. <i>Castianeira cingulata</i> C. L. Koch | | | | | D | LO | ASX |
| 50. <i>Castianeira descripta</i> Hentz | | | | | W | | U |
| 51. <i>Castianeira longipalpus</i> Hentz | | | | | K | | SX |
| 52. <i>Castianeira trilineata</i> Hentz | | | | | DK | | |
| 53. <i>Cheiracanthium inclusum</i> Hentz | | | | | K | | |
| 54. <i>Clubiona obesa</i> Hentz | | | | | W | | S |
| 55. <i>Clubiona pallens</i> Hentz | | U | O | O | D | L | ASX |
| 56. <i>Clubiona riparia</i> L. Koch | | | | | W | | |
| 57. <i>Clubiona saltitans</i> Emerton | | | | | K | | |
| 58. <i>Micaria aurata</i> Hentz | | | | | WD | | |
| 59. <i>Phrurolithus formica</i> Banks | | | | | K | | |
| 60. <i>Phrurolithus alarius</i> Hentz | | | | | KO | O | X |
| 61. <i>Phrurolithus kentuckyense</i> Chamberlin & Gertsch | | | | | | | A |
| 62. <i>Phrurolithus palustris</i> Banks | | | | | W | | X |
| 63. <i>Trachelas tranquillus</i> Hentz | | | | | D | | X |

TABLE I—Continued

| Species | B | F | C | P | O | S | B-M |
|--|-----|------|------|---|-------|----|------|
| Dictynidae | | | | | | | |
| 64. <i>Dictyna bicornis</i> Emerton | | WDO | WULO | O | | | |
| 65. <i>Dictyna bostoniensis</i> Emerton | | | | O | | | |
| 66. <i>Dictyna foliacea</i> Hentz | | | | O | OD | OL | ASUX |
| 67. <i>Dictyna frondea</i> Emerton | | | | O | WDK | | |
| 68. <i>Dictyna volucris</i> Keyserling | | | | O | WDK | | S |
| Dysderidae | | | | | | | |
| 69. <i>Dysdera crocata</i> C. L. Koch | | | | | K | | |
| Gnaphosidae | | | | | | | |
| 70. <i>Callilepis imbecilla</i> Keyserling | D | D | | O | DKO | | |
| 71. <i>Cesonia bilineata</i> Hentz | | | | | W | | |
| 72. <i>Drassodes neglectus</i> Keyserling | | | | | WDK | | |
| 73. <i>Drassodes robinsoni</i> Chamberlin | | | | | WK | | |
| 74. <i>Drassylus depressus</i> Emerton | | | | | K | | |
| 75. <i>Drassylus rufulus</i> Banks | | | | O | K | | S |
| 76. <i>Gnaphosa sericata</i> L. Koch | | | | | | | S |
| 77. <i>Haplodrassus bicornis</i> Emerton | | | | | | | S |
| 78. <i>Haplodrassus signifer</i> C. L. Koch | | | | | DKM | | S |
| 79. <i>Herpyllus vasifer</i> Walckenaer | W | | | O | WDK | O | AX |
| 80. <i>Poecilochroa montana</i> Emerton | | | | | K | | |
| 81. <i>Sosticus insularis</i> Banks | | | | | D | | A |
| 82. <i>Sergiolus variegatus</i> Hentz | | | | | | | UX |
| 83. <i>Zelotes subterraneus</i> C. L. Koch | | | | | WK | | X |
| Hahnidae | | | | | | | |
| 84. <i>Hahnia cinerea</i> Emerton | | | | | O | O | X |
| 85. <i>Neoantistea agilis</i> Keyserling | | | | | W | | X |
| 86. <i>Neoantistea riparia radula</i> Keyserling | | | | | | | ASX |
| Linyphiidae | | | | | | | |
| 87. <i>Bathypantes formica</i> Emerton | | WDK | | | | | |
| 88. <i>Bathypantes nigrinus</i> Westring | | W | | | WD | | X |
| 89. <i>Bathypantes subalpinus</i> Emerton | | | | | | | A |
| 90. <i>Frontinella coccinea</i> Hentz | | | | | K | | |
| 91. <i>Frontinella communis</i> Hentz | | | | | | | S |
| 92. <i>Helophora insignis</i> Blackwall | | | | | | | A |
| 93. <i>Linyphia clathrata</i> Sundevall | | | | | | O | ASX |
| 94. <i>Linyphia maculata</i> Emerton | | | | | | | SX |
| 95. <i>Linyphia marginata</i> C. L. Koch | | | | | K | | ASUX |
| 96. <i>Linyphia pusilla</i> Sundevall | | | | | D | | |
| 97. <i>Pityohyphantes phrygiana</i> C. L. Koch | | | | | D | OL | ASX |
| Lycosidae | | | | | | | |
| 98. <i>Arctosa emertoni</i> Gertsch | | | | | W | | |
| 99. <i>Arctosa littoralis</i> Hentz | WDO | WDLM | | | K | | |
| 100. <i>Geolycosa missouriensis</i> Banks | | | | | WDK | | |
| 101. <i>Geolycosa wrightii</i> Emerton | WD | WDOL | WDO | O | K | | |
| 102. <i>Lycosa aspersa</i> Hentz | | | | | OD | | S |
| 103. <i>Lycosa avara</i> Keyserling | | | | | WDK | | A |
| 104. <i>Lycosa ballimoriana</i> Keyserling | | | | | WDK | | |
| 105. <i>Lycosa carolinensis</i> Walckenaer | | | | | K | | |
| 106. <i>Lycosa frondicola</i> Emerton | | | | | WDKOM | | |
| 107. <i>Lycosa gulosa</i> Emerton | | | | | | | ASX |
| 108. <i>Lycosa helluo</i> Walckenaer | O | | | | WDK | | |
| 109. <i>Lycosa permunda</i> Chamberlin | | | | | | | S |
| 110. <i>Lycosa rabida</i> Walckenaer | O | | | | DK | | SX |
| 111. <i>Pardosa fuscata</i> Thorell | | | | | D | | |
| 112. <i>Pardosa milvina</i> Hentz | OM | O | | | WDK | | AS |
| 113. <i>Pardosa modica</i> Blackwall | | | | | W | | |
| 114. <i>Pardosa moesta</i> Banks | | | | | WD | | |
| 115. <i>Pardosa saxatilis</i> Hentz | | | | | W | | |
| 116. <i>Pirata piratica</i> Olivier | WO | | O | | WDK | | SX |
| 117. <i>Pirata insularis</i> Emerton | WO | | | | W | | S |
| 118. <i>Pirata marxi</i> Stone | | | | | | | S |
| 119. <i>Pirata montanus</i> Emerton | W | | | | | | |
| 120. <i>Schizocosa avida</i> Walckenaer | OM | OW | | | WDK | | A |
| 121. <i>Schizocosa bilineata</i> Emerton | | | | | W | | |
| 122. <i>Schizocosa crassipes</i> Walckenaer | | | | | D | L | ASX |
| 123. <i>Schizocosa retrorsa</i> Banks | | | | | W | | |
| 124. <i>Schizocosa saltatrix</i> Hentz | | | | | DKO | | |
| 125. <i>Trochosa shenandoa</i> Chamberlin & Ivie | | | | | K | | |
| Micryphantidae | | | | | | | |
| 126. <i>Ceraticelus emertoni</i> O. P.—Cambridge | | | | O | WDK | | S |
| 127. <i>Ceraticelus fissiceps</i> O. P.—Cambridge | | | | O | D | O | |
| 128. <i>Ceraticelus limnologicus</i> Crosby & Bishop | | O. | | | DK | | |
| 129. <i>Ceraticelus minutus</i> Emerton | | | | | | O | X |
| 130. <i>Ceraticelus similis</i> Banks | | | | | W | | |
| 131. <i>Ceratinopsis anglicana</i> Hentz | | | | | | LD | A |
| 132. <i>Erigone atra</i> Blackwall | W | | | | | | |
| 133. <i>Erigone autumnalis</i> Emerton | | | | | DK | | |
| 134. <i>Erigone dentigera</i> Chamberlin | | D | | | | | |
| 135. <i>Hypselistes florens</i> O. P.—Cambridge | | | | | D | | S |
| 136. <i>Minyriolus arenarius</i> Emerton | | | | | W | | |
| 137. <i>Oodothorax bidentatus</i> Emerton | | | | | W | | |
| Mimetidae | | | | | | | |
| 138. <i>Ero urcata</i> Villiers | | | | | | O | X |
| 139. <i>Mimetus intersector</i> Hentz | | | | | | O | S |
| Oxyopidae | | | | | | | |
| 140. <i>Oxyopes salticus</i> Hentz | | | | | WDK | | A |

TABLE I—Continued

| Species | B | F | C | P | O | S | B-M |
|---|-----|------|-----|----|-------|-----|------|
| Pisauridae | | | | | | | |
| 141. <i>Dolomedes scriptus</i> Hentz | | | | | D | L | A |
| 142. <i>Dolomedes striatus</i> Becker | | | | | DK | | |
| 143. <i>Dolomedes tenebrosus</i> Hentz | | | | | D | | ASX |
| 144. <i>Dolomedes triton sexpunctatus</i> Hentz | | | | | WDK | | |
| 145. <i>Pisaurina brevipes</i> Emerton | | | | | W | | AS |
| 146. <i>Pisaurina mira</i> Walckenaer | | | | | WD | OD | ASX |
| Salticidae | | | | | | | |
| 147. <i>Admetina tibialis</i> C. L. Koch | | | | O | K | | S |
| 148. <i>Evarcha hoyi</i> Peckham | | | | | D | | |
| 149. <i>Habrocestum pulex</i> Hentz | | | | | KO | | ASUX |
| 150. <i>Hentzia mirata</i> Hentz | | | | | D | DLO | S |
| 151. <i>Hentzia palmarum</i> Hentz | | | | | D | DO | |
| 152. <i>Hycitia pikei</i> Peckham | | | | | W | | SX |
| 153. <i>Icius hartii</i> Emerton | | | | | WK | | U |
| 154. <i>Icius similis</i> Banks | | | | | K | | ASDX |
| 155. <i>Maevia vittata</i> Hentz | | W | | O | DKO | O | S |
| 156. <i>Marpissa undata</i> DeGeer | | | | | | | |
| 157. <i>Metaphidippus flavus</i> Peckham | | | | | WD | | |
| 158. <i>Metaphidippus galathea</i> Walckenaer | UW | | LO | OU | WK | L | UX |
| 159. <i>Metaphidippus protervus</i> Walckenaer | | | | | WK | L | S |
| 160. <i>Paraphidippus marginatus</i> Walckenaer | | | | O | WDK | LO | S |
| 161. <i>Pechhamia scorpionea</i> Hentz | | | | | WK | | |
| 162. <i>Pellenes agilis</i> Banks | WD | | WD | OU | WDK | | U |
| 163. <i>Pellenes arizoniensis</i> Banks | | | | O | K | | |
| 164. <i>Pellenes borealis</i> Banks | OWD | | OWD | | | | |
| 165. <i>Pellenes calcaratus</i> Banks | | | | | DKO | | |
| 166. <i>Pellenes viridipes</i> Hentz | | | | | WK | | |
| 167. <i>Pellenes</i> sp. nov. | | | | | DK | | |
| 168. <i>Phidippus audax</i> Hentz | | | | O | WDKOL | | ASX |
| 169. <i>Phidippus brunneus</i> Hentz | | | | | WDK | | S |
| 170. <i>Phidippus clarus</i> Keyserling | | | | | WDK | O | SX |
| 171. <i>Phidippus insignarius</i> C. L. Koch | W | | WDO | O | WDK | | S |
| 172. <i>Phidippus mccoeki</i> Peckham | D | | D | | WD | | |
| 173. <i>Phidippus whilmani</i> Peckham | | | | | K | | |
| 174. <i>Sidusa borealis</i> Banks | | | | | DK | | |
| 175. <i>Sittacus palustris</i> Peckham | | | | | WD | O | |
| 176. <i>Talavera minuta</i> Banks | | | | O | | | |
| 177. <i>Tutelina elegans</i> Hentz | | | | | DK | | S |
| 178. <i>Zygoballus bellini</i> Peckham | | | | | DK | | S |
| 179. <i>Zygoballus nervosus</i> Peckham | OW | D | | | | | |
| Theridiidae | O | O | | | | O | X |
| 180. <i>Crustulina guttata</i> Wider | | | | | K | | |
| 181. <i>Enoplognatha marmorata</i> Hentz | | | | | O | | |
| 182. <i>Euryopsis argentea</i> Emerton | | | | | W | | |
| 183. <i>Euryopsis funebris</i> Hentz | | | | | DKL | L | SX |
| 184. <i>Latrodectus mactans</i> Fabricius | | | L | O | WDK | | |
| 185. <i>Lithyphantes albomaculatus</i> DeGeer | | | OU | O | | | |
| 186. <i>Robertus riparius</i> Keyserling | | | | O | W | O | |
| 187. <i>Steatoda borealis</i> Hentz | | | | O | | L | ASX |
| 188. <i>Theridion cinereum</i> Emerton | | | | O | WD | OL | S |
| 189. <i>Theridion differens</i> Emerton | | | | | D | O | AUX |
| 190. <i>Theridion frondeum</i> Hentz | | | | | | | ASX |
| 191. <i>Theridion globosum</i> Hentz | | | | | | | U |
| 192. <i>Theridion kentuckyense</i> Keyserling | | | | | | | A |
| 193. <i>Theridion murarium</i> Emerton | | | | O | WD | O | ASU |
| 194. <i>Theridion rupicola</i> Emerton | | | | | | | AS |
| 195. <i>Theridion spirale</i> Emerton | | | | | | | U |
| 196. <i>Theridion lepidarium</i> C. L. Koch | | | | | W | | S |
| 197. <i>Theridion unimaculatum</i> Emerton | | | | | | | S |
| 198. <i>Ulesanis americana</i> Emerton | | | | | | | AS |
| Thomisidae | | | | | | | |
| 199. <i>Coriarachne versicolor</i> Keyserling | | | | O | DKO | O | S |
| 200. <i>Ebo latithorax</i> Keyserling | | D | | | | | |
| 201. <i>Ebo pepinensis</i> Gertsch | | | O | O | W | | |
| 202. <i>Misumenoides aleatorius</i> Hentz | | | | O | WDK | | S |
| 203. <i>Misumenops asperatus</i> Hentz | | | | O | WDK | O | SDX |
| 204. <i>Misumenops celer</i> Hentz | | | | O | W | | |
| 205. <i>Misumenops oblongus</i> Keyserling | | | | | WDK | L | SX |
| 206. <i>Oxytala americana</i> Banks | | | | | | | S |
| 207. <i>Philodromus alascensis</i> Keyserling | | LOWD | O | O | | | |
| 208. <i>Philodromus aureolus</i> Olivier | | OWD | W | O | WD | | U |
| 209. <i>Philodromus imbecillus</i> Keyserling | | | | | W | | |
| 210. <i>Philodromus infuscatus</i> Keyserling | | | | | K | | |
| 211. <i>Philodromus ornatus</i> Keyserling | | | | | | | S |
| 212. <i>Philodromus permix</i> Blackwall | W | | | O | WDKO | | |
| 213. <i>Philodromus rufus</i> Walckenaer | | | | | | DL | |
| 214. <i>Philodromus thorelli</i> Marx | | | | | D | | |
| 215. <i>Thanatus</i> immature | | | O | O | WKO | | |
| 216. <i>Tibellus duttoni</i> Hentz | | | | | K | | |
| 217. <i>Tibellus maritimus</i> Menge | | | | | WD | | |
| 218. <i>Tibellus oblongus</i> Walckenaer | | | | | WDK | | S |
| 219. <i>Tmarus angulatus</i> Walckenaer | | | | | | O | ASD |
| 220. <i>Xysticus banksi</i> Bryant | W | | | | W | | S |
| 221. <i>Xysticus elegans</i> Keyserling | | | | | KM | L | SU |
| 222. <i>Xysticus ferox</i> Hentz | | | | | K | | ASUX |

TABLE I—Continued

| Species | B | F | C | P | O | S | B-M |
|---|----|----|----|----|------|----|-----|
| Thomisidae—Continued | | | | | | | |
| 223. <i>Xysticus fraternus</i> Banks | | | | O | WDKO | O | ASX |
| 224. <i>Xysticus gulosus</i> Keyserling | | W | | | WDK | O | S |
| 225. <i>Xysticus luctans</i> Keyserling | | | | | WK | | |
| 226. <i>Xysticus triguttatus</i> Keyserling | | W | | | WDKO | | |
| Uloboridae | | | | | | | |
| 227. <i>Hyptioles cavatus</i> Hentz | | | | | | O | ASX |
| 228. <i>Uloborus americanus</i> Walckenaer | | | | | | O | SUX |
| Total number of species | 17 | 31 | 18 | 43 | 168 | 56 | 122 |

Number of species found at Kankakee only—26.

Number of species found at Waukegan only—28.

Number of species found at Kankakee and Waukegan only—8.

Elliott lists 98 species found in Lewis Woods.

47 of these were found in the present study in the climax also.

11 of these were not found in the climax in the present study but were found in earlier associates.

41 species were not found in the present study.

more characteristic of this associates than any other species, as it is found on the marram grass, *Ammophila arenaria*, where it builds a small silken retreat in the spikes. Of the salticids, *Pellenes borealis*, a gray, sand-colored species, is nearly as common as *Philodromus alascensis*. Eight hundred sweeps in the fore-dune contained 19 specimens of *Pellenes borealis* in contrast with 75 of *Philodromus alascensis* (table IV). Other species found in the fore-dune are not so common or characteristic, though there is an increase in the number of species and individuals of salticids and thomisids. The four characteristic species of this associates are *Philodromus alascensis*, *Pellenes borealis*, *Dictyna bostoniensis*, and *Geolycosa wrightii*. The associates might be named for any of these species, though *Philodromus alascensis* is probably confined to this associates more than any of the other species.

THE COTTONWOOD DUNE: Except for the addition of the dominant *Populus deltoides* Marshall, this area is similar to the above as far as the plant members are concerned. This addition changes the spider fauna but little, as it does not seem to add enough in the way of support or protection from the sun to allow many additional species to establish themselves. All of the species of the fore-dune will probably be found here, though collecting as yet has not disclosed their presence.

There are no important additions to this associates. *Lithyphantes albomaculatus*, *Ebo pepinensis* and *Thanatus* sp. are the only additional species, and they are rare; they will probably be found eventually in the fore-dune. Therefore, as far as the spiders are concerned, it seems that this associates is not definitely distinguishable from the fore-dune.

THE PINE: The dominant plant of this associates is *Pinus banksiana* Lamb. The factors involved in the formation of this community are physical as is also largely true of the preceding stages. Here, however, the greater distance from the lake and the protection afforded by the cottonwood dunes is most effective in providing a suitable place for pine growth. All of the families of spiders increase in number of species in this associates (particularly the dictynids, salticids, theridiids, and thomisids). Most of the newcomers are found in the herbaceous layer; the dictynids are common on leaves of false solomon's seal.

THE BLACK OAK: As the common name indicates, this community is dominated by the oak *Quercus velutina* Lam- arck. Considerably more undergrowth is found here than in the pine associates. This associates has been more thoroughly studied than any other in the comparison of the Kankakee, Waukegan, and Indiana black oak regions (Lowrie, '42), and the number of species found in this associates is the

greatest of those found in any one associates and is probably proportionately greater than in other associates. One hundred sixty-eight species have been found here in contrast with forty-three in the pine (table I), but there are undoubtedly still more species to be found in the pine. In this study for the first time, in the succession, the cinifluids, hahniids, linyphiids, mimetids, oxyopids, and pisaurids are found; all of the other families increase in number of species. In general, therefore, this associates may be characterized by the great increase in the total number of spiders and diversity of forms; no one species can be designated as dominant.

THE RED OAK-WHITE OAK: This associates was not investigated in this study.

THE SUBCLIMAX: This community is not well represented in the present work. The Lakeside and Ogden Dunes associates, which are subclimaxes on sand, were the areas studied. The subclimax is characterized by a mixture of such trees as beech, maple, linden and witch-hazel. Several of the characteristic climax forms are now found for the first time in the succession in this study. *Aranea raji*, and *Mangora maculata* and the two uloborids are typical of the more moist woods where there is a minimum of air movement. They are forerunners of the climax.

THE BEECH-MAPLE CLIMAX: In this associates were found the second greatest number of species of spiders. As represented by the beech-maple forests of Saugatuck and Warren's Woods, Michigan, and Smith, Indiana, and various swales at Dune Acres, the number is not greater than that of the Black Oak which has been much more completely collected (15 trips to climax forests: 24 trips to the black oak at Dune Acres). The web-building species are in nearly equal abundance here and in the black oak but there are only about one half as many ground dwelling species (table II).

Characteristic species belong to the Argiopidae, Agelenidae, Linyphiidae, Pisauridae, Theridiidae and Uloboridae.

Aranea raji, *Micrathena sagittata*, *Theridiosoma radiosum*, most Linyphiidae, *Dolomedes tenebrosus*, various *Theridiids*, and two species of uloborids are among the most common and characteristic species of this associates. The lycosids, salticids, and thomisids are here in less abundance than in the black oak but undoubtedly some of them are unique climax forms. Of interest in regard to the beech-maple spiders is the large number of species involved. Shelford ('13) has shown that the fauna of the climax forest is not as great as in the preceding stages. The herbaceous layer is less prominent. This should reduce the number of spiders as well as the number of other kinds of animals. The logical reason for the apparently large spider fauna is the fact that the beech-maple woods are not extensive anywhere in the Chicago area; many species undoubtedly wander into and through the area although they are not truly typical. Also, the climax forests studied do not seem to be as free from herbaceous vegetation as was true of the forests when they were more extensive. Moreover, the small size of the woods makes it impossible to exclude ecotone species which may penetrate into most of an area which is only a quarter or a half square mile.

LOG SUCCESSION

There is a succession of spiders in logs as is shown by this investigation. Stumps and logs in early stages of decay, or in any stage in which the general shape is retained, might harbor beneath loose bark during the day *Herpyllus vasifer*, *Dolomedes tenebrosus*, *Coriarachne versicolor*, or *Philodromus pernix*. The *Dolomedes* have been observed to remain hidden under loose bark or in the cavities of fallen logs during the day, issuing forth at night to feed. Hibernating groups of species of *Philodromus* or various Gnaphosidae might be found during the winter. In addition, most of the linyphiids may build their webs in the shelter of logs, and any of the free-running species crawl about in

TABLE II. *Number of species of each family found in each associes*

The first figure under each associes is for the total area collected. The second figure under each associes is for those species collected in the Michigan-Indiana area only.

| | Beach | Fore-dune | Cotton-wood | Pine | Oak | Sub-climax | Climax | Total |
|--|-------|-----------|-------------|-------|--------|------------|---------|---------|
| 1. Agelenidae | | | | 1-1 | 3-1 | 3-3 | 8-8 | 9-8 |
| 2. Argiopidae | 2-1 | 5-5 | 3-3 | 5-5 | 26-18 | 5-5 | 20-20 | 31-27 |
| 3. Cniflonidae | | | | | 1-1 | 1-1 | 1-1 | 2-2 |
| 4. Dictynidae | | 1-1 | 1-1 | 4-4 | 3-3 | 1-1 | 2-2 | 5-5 |
| 5. Hahniidae | | | | | 2-1 | 1-1 | 1-1 | 3-2 |
| 6. Linyphiidae | | 2-0 | | | 5-3 | 2-2 | 7-7 | 11-9 |
| 7. Micryphantidae | 2-1 | 2-2 | | 2-2 | 8-4 | 3-3 | 3-3 | 12-8 |
| 8. Mimetidae | | | | | 1-1 | 2-2 | 1-1 | 2-2 |
| 9. Theridiidae | 1-1 | 1-1 | 2-1 | 5-5 | 10-6 | 7-7 | 13-13 | 19-18 |
| 10. Uloboridae | | | | | | 2-2 | 2-2 | 2-2 |
| Total web-builders | 5-3 | 11-9 | 6-5 | 17-17 | 59-38 | 27-27 | 58-58 | 96-84 |
| Per cent web-builders found in associes | 5-4 | 12-11 | 7-6 | 18-20 | 61-45 | 28-32 | 60-69 | 42-45 |
| Per cent of species found in associes that are web-builders | 29-23 | 35-39 | 34-31 | 40-39 | 35-39 | 48-48 | 48-47 | |
| 11. Anyphaenidae | | | | 1-1 | 1-1 | 3-3 | 3-3 | 3-3 |
| 12. Atypidae | | | | | | 1-1 | | 1-1 |
| 13. Clubionidae | | 1-1 | 1-1 | 1-1 | 14-6 | 5-5 | 7-7 | 17-12 |
| 14. Dysderidae | | | | | 1-0 | | | 1-0 |
| 15. Gnaphosidae | 2-1 | 1-1 | | 3-3 | 11-5 | 1-1 | 6-6 | 14-9 |
| 16. Lycosidae | 9-8 | 4-4 | 2-2 | 1-1 | 24-12 | 1-1 | 11-11 | 28-19 |
| 17. Oxyopidae | | | | | 1-1 | | 1-1 | 1-1 |
| 18. Pisauridae | | | | | 6-5 | 2-2 | 4-4 | 6-6 |
| 19. Salticidae | 1-1 | 7-5 | 5-5 | 10-10 | 29-18 | 8-8 | 17-17 | 33-27 |
| 20. Thomisidae | | 7-3 | 4-3 | 10-10 | 22-12 | 8-8 | 14-14 | 28-23 |
| Total non-web-builders | 12-10 | 20-14 | 12-11 | 26-26 | 109-60 | 29-29 | 63-63 | 132-102 |
| Per cent species found in associes that are non-web-builders | 71-77 | 65-61 | 66-69 | 60-61 | 65-61 | 52-52 | 52-53 | 58-55 |
| Total number of species | 17-13 | 31-23 | 18-16 | 43-43 | 168-98 | 56-56 | 122-122 | 228-186 |
| Per cent of total species found in each associes | 7-7 | 14-12 | 8-4 | 19-22 | 74-53 | 25-30 | 54-65 | |
| Per cent of non-web-builders found in each associes | 9-10 | 15-14 | 9-11 | 20-25 | 83-59 | 22-28 | 48-62 | |

and on logs during the night and even in the daytime. A log in intermediate stages of decay, with a hollow center forms a convenient cavity for the webs of ciniflonids and agelenids in particular. Members of the genus *Castianeira*, as well as various other clubionids and gnaphosids may also be found in hollow logs. *Steatoda* also seems to be mainly a log inhabitant in this area, building its web in the cavities.

Lastly, there are the free-running lycosids and salticids which make a tem-

porary home in logs or beneath loose bark, but which are not obligatory log dwellers; they may be found in any stage of log decay. Thus, as far as spiders are concerned, there seems to be only three stages in the log succession. A first stage is that which presents crevices and burrows in the wood for the flattened types like *Coriarachne versicolor*; an intermediate stage, is that in which there are larger cavities which are used by the more characteristic ciniflonid and agelenid log dwellers; and a third stage is that which

is much like the first with mainly free-running species, but possibly with fewer characteristic species, as there is less in the way of cover to harbor such vagabond types when the log is reduced to a crumbling mass.

STRATIFICATION

Stratification in the woods is part of the answer to the question as to why there is an increase in the number of species as one goes from the open beach to the complex stratified advanced stages. Stratification means an increased area of substratum with a corresponding increase in the number of habitat niches. For example, most of the thomisids are lacking on the beach and foredune, in the cottonwood, and even to quite an extent in the pine, due, in part, to the fact that many of these spiders are flower inhabitants; i.e., they are members of the herb stratum which is lacking, or greatly reduced, in the early stages of the succession. Elliott ('30) has made a study of this phase of the spider distribution in a beech-maple forest. He has shown that there is a distinct stratification which varies with the seasons as well as a condition of zones on the horizontal plane. The herb-shrub forms are mainly web-builders (only four—*Icius hartii*, *Misumenops asperatus*, *Philodromus minutus* and *Tmarus* sp. (*caudatus*?) are non-web-builders). In contrast, the ground floor forms are a much more mixed group containing many vagabond species. At least seventeen of the forty-one species listed must be considered as non-web-builders, while over half of those remaining build virtually no webs. The seasonal distribution shows much the same sort of stratification. The winter forms are ground dwellers which do not build webs. As the season advances, more and more web-builders appear, invading the herbs and finally the shrubs. In a previous quantitative study of the spiders of the dunes (Lowrie, '42), an analysis of sweepings of the black oak dunes was made showing the herb-shrub layers to be of importance.

Of particular interest was the lack of lycosids; only 9 of the 2784 specimens were of this family. Later work not yet reported indicates that this number would be much greater at night as the lycosids move up into the stratum, probably searching for food. The scarcity of gnaphosids and anyphaenids is also of significance; this scarcity indicates that these families are not often found at the herb level, at least in these dry, open lands during the day. The reduction in number of argiopids, dictynids, and theridiids may also be an expression of their greater abundance in the shrub-tree stratum, though probably it is also coupled with the drier conditions in the open oak dune.

It is apparent from these few remarks that the problem of stratification is of decided importance in the dunes succession of spiders, though in this work the problem has not been studied in detail.

WEB-BUILDERS AND NON-WEB-BUILDERS

In this study the spiders have been separated according to these two categories (tables II and IV) in an attempt to correlate distribution with available substratum. The web-builder category includes those families in which the species build extensive webs as living quarters or for catching prey. The species of argiopids, linyphiids, theridiids, uloborids, and mimeids (invaders of webs of theridiids and other web-builders) in the main require rather substantial substrata for their webs and themselves. In one way this is less true of the ciniflonids, dictynids, hahniids, and micryphantids, as these are all small spiders generally requiring little in the way of substratum. They are all more or less dependent directly or indirectly upon herbaceous plants, trees, or shrubs for their webs so that, in spite of their size, they are dependent upon vegetation for a substratum. The agelenids fit into the non-web-building category to some extent as some of the forms are found outside of their webs much of the time.

The non-web-building category contains the anyphaenids, atypids, clubionids

and gnaphosids many of which do construct a small retreat in which they rest or spend their quiescent period each day. Their webs, however, depend on very little in the way of substratum and are often built beneath stones, in dead leaves, etc. The lycosids, oxyopids, pisaurids, salticids, and thomisids are all quite definitely to be placed in this category even though some of them also build some semblance of silken retreats or tubes, most often with their eggs and only at that season.

BIOTIC FACTORS

Other animals as food and enemies are of importance, but probably they are not limiting factors as much as are some of the physical conditions. As has been shown by most workers, the number of insects and other animals increases from the beach to the subclimax forest (Shelford, '13; Downing, '22, etc.). As spiders are entirely carnivorous, this increase is of importance, as it will allow more individuals to exist in the same unit area, at least as regards available food. Therefore, this factor would tend to increase the number of individuals, and possibly the number of species. On the other hand the spider wasps, birds, and other enemies of the spider would tend to increase as well, and thus there would be a partial balancing of the effect of increased prey. These factors are unfortunately quite difficult to treat in any satisfactory manner, but nevertheless, must be operative. The specific available food supply is possibly of importance as Bristowe ('39) has shown that some spiders are specific in their food habits.

PHYSICAL FACTORS

The physical factors may be tested much more satisfactorily in a quantitative fashion than the biotic factors. However, there are many gaps in the studies which have been made in regard to evaporation, temperature, and the like as far as their significance in this study are concerned.

SUBSTRATUM: The matter of substra-

tum has not been treated quantitatively by anyone though it is quite obviously of major importance in the lives of spiders. There is virtually no plant growth on the beach; an increase on the foredune with the advent of the beach grasses, still more with the cottonwoods and pine and so on. The subclimax has the greatest amount of ground cover, herbs, shrubs, and trees. This increased scaffolding area for building of webs and for cover in the leaf mold is certainly of prime importance, as it would be impossible for most of the large argiopids, for example, to build webs unless the pine stage were reached, as there isn't sufficient support for the webs until an area has developed trees which are set closely enough together for web construction from tree to tree and for protection as a windbreak. The increase of trees also means increase of logs as habitat niches for the ciniflonids, lycosids, agelenids, clubionids, etc. Thus it is apparent that the increased amount of vegetation parallels the increased number of web-builders, while the increased leaf mold also adds niches for additional species. This does not apply to the climax forest in which the vegetation is reduced.

EVAPORATION: Moisture in all its aspects is of prime importance to spiders. The importance of evaporation, however, cannot be properly evaluated until much more work has been done. Weese ('24) has shown the importance of evaporation rate for several species of spiders. Fuller ('14), using the Livingston atmometer, has shown about 23 cc. mean daily average evaporation in the cottonwoods, 10.5 cc. in pine, 11 cc. in black oak, 9 cc. in oak-hickory, and 7 cc. in the beech-maple. These measurements were made at a height of 20 to 25 centimeters above the ground. For adequate analysis for use in this work, ground floor evaporation rates as well as the rate at various heights up to 15 or 20 feet would be more useful than the one measurement made by Fuller. However, the general trend of increased moisture in the air as the climax is reached, is shown by these data. Fuller

('14) shows from atmometer readings, at two meters in the climax forest, that the evaporation is greater than at the 25 cm. level, especially early in the summer, but is still much less than that of the other associates.

SOIL MOISTURE: This is of importance to the ground inhabiting species, especially the burrowers. Again, it is shown that the climax ground has the greatest soil moisture. Fuller ('12, '14) found 4.4 per cent of dry weight in the climax forest to be growth-water. Growth-water is that which is available to plants and is thus an expression of the moisture of the soil. Fuller found that the layer of dry sand an inch or two thick covering the surface preserved the deeper water, so that in the cottonwood where there is a scarcity of vegetation, there was more growth-water (about half of that of the climax) than in the pine and black oak (about one-third or less of that of the climax). This may account for the presence of *Geolycosa wrightii* which requires more moisture than most species. Specimens kept in the laboratory without water or damp sand in their cells will die within a day. This is in contrast with such species as *Latrodectus mactans* which lives indefinitely in the laboratory without having water placed in the cell, and seems to prefer dry, well-drained areas (Semans '41).

TEMPERATURES: Strohecker ('37a) has shown that the temperature maximum for the foredune, cottonwood, and pine dunes was 64° C. at the soil surface; 38° was the maximum in the black oak; and 24° in the climax forest. The minimum soil temperatures at a depth of two inches were nearly the same for all associates so that the burrowing species could reach a depth where hibernation or avoidance of excessive midday heat would be possible in any of the associates. The non-burrowing forms apparently avoid the high temperatures by keeping in the shade of vegetation.

WIND VELOCITY: Wind is an important factor in the distribution of spiders which

build webs. Many of the webs are so delicate that a strong wind would destroy them. The beach, foredune and cottonwood are open to nearly the full effects of the wind. In the pine associates there is an element of protection, as this associates is usually protected by the shoreward dunes and by the resistance of the trees themselves. Oak dunes, with greater undergrowth, offer still more resistance, while the climax forests offer the most resistance to wind and are thus suitable for the webs of *Mangora maculata* and many other argiopids, linyphiids and theridiids whose fragile webs could not withstand the storm winds of the earlier associates.

LIGHT: Light has various effects upon animals. Lighter colored animals are found in areas continually exposed to the sun. Where there is a minimum of light and more humid conditions, coloration tends to become darker (Hesse, Allee and Schmidt, p. 379). Park ('31) and Strohecker ('38) have shown that there is a decrease in light intensity from the beach toward the climax, as might be expected. The spiders of the earlier associates tend to be lighter in color than those of the climax. Specific counts of the number and proportion of species and individuals which are light colored in beach versus climax associates have not been made. General observation of the beach, climax and other associates species, however, indicate that beach thru cottonwood species are light colored. Light may not be the cause of this coloration, but certainly it is correlated with it. These phases of the effects of light are probably only indirectly connected with the spider distribution. Sunlight is most important because it indirectly produces heat and increases evaporation, thus lowering the relative humidity. These effects were discussed earlier.

Also of importance is the night and day effect of light. Many spiders are nocturnal—lycosids, many argiopids, clubionids, etc. No detailed study of these forms has been made, so that the period

of activity of all these species is not known. The diurnal forms are usually those with good eyesight such as thomisids and salticids, though many linyphiids, theridiids, and argiopids—essentially tactilily dependent, not visually dependent forms—are often equally active. In addition to these two types there is a third group of species which are irregularly active. Many of the web-builders come in this category, as they catch prey which falls into the web. This is apt to happen either during the day or night. Between catches these spiders do some web repairing but otherwise are mainly inactive.

DISTRIBUTION OF FAMILIES

AGELENIDAE: The funnel-web spiders build webs which they inhabit as long as they catch prey, adding to the sheet-like web daily, so that an old web is a substantial structure. Members of the genus *Coras* are largely log dwellers. Thus all of these species must find an area of rather stable vegetation on which to build. Moisture requirements would seem to be fairly high for most of these species. Substratum in the form of bushes or shrubs is necessary for the building of the webs which usually are only one or two feet above the ground. Therefore, these spiders are virtually eliminated from any earlier stages than the oak or pine dune and even there are very rare.

CINIFLONIDAE: These species are log dwellers which are largely eliminated from the stages earlier than the oak by the scarcity of a suitable habitat.

ANYPHAENIDAE: Except for *Aysha gracilis*, this family is restricted to the climax and subclimax. *A. gracilis* is found in the herb stratum. The family is quite similar to the clubionids in habits.

ARGIOPIDAE: In general, these builders of the beautiful, symmetrical wheel-shaped orb webs are lacking in any stage before the pine. Even here, there are only a few species. *Eustala anastera* and *Tetragnatha laboriosa* are quite wide-ranging forms in the Chicago area. Both are

small spiders requiring very little support for their webs. They are apparently quite tolerant of moisture and temperature extremes. A related species, *Mangora gibberosa* (*Epeira gibberosa*), has been shown by Weese ('24) to have a fairly wide tolerance for humidity. The same is probably true of these species, as well as *Neoscona arabesca*, which is also found from the pine into the climax and elsewhere in the Chicago area. Six species are restricted to the climax forest and most of the others are found there in greater abundance than in the earlier stages. Thus, it is apparent that the argiopids may be divided into a black oak-climax group and a small ubiquitous group. More work will probably show the climax species to be more extensive in their distribution.

ATYPIDAE: The only species (*Atypus milberti*) of this group found in the Chicago area has been collected but once in the Lakeside subclimax forest. It is a southern species but can not be definitely associated with any specific stage in the dunes succession at the present state of our knowledge.

CLUBIONIDAE: These spiders are largely ground-floor and herbaceous forms. The lack of cover on the ground in earlier stages is one factor which has kept them confined to the intermediate associates. Probably humidity is also important, as specimens which were kept alive in the laboratory had to have water constantly available. One species, *Clubiona obesa*, is cosmopolitan and common throughout the Chicago area.

DICTYNIDAE: The dictynids are found in the crevices of tree trunks and on herbaceous plants, particularly on the upper surface of leaves along the mid-rib near the petiole. Their webs are flat covering the crevices of the tree trunk. These substrata restrict them to black oak or more complex stages; moisture may also be a factor. One species, *Dictyna bostoniensis*, has been found in large numbers on cottonwoods where branches form an angle for the web.

GNAPHOSIDAE: This group is similar in habitat to the clubionids, except that they are restricted more completely to the ground floor. This family has not been well worked in this study as no quadrat studies or other particularly intensive investigations of the ground floor were made. Two species, *Callilepis imbecilla* and *Herpyllus vasifer*, are common elsewhere in the Chicago region.

HAHNIIDAE: The Hahniidae is a small family of tiny spiders which build webs amongst the leaf mold of the ground floor. Therefore, they are excluded from all but the last stages, where the leaf mold is to be found.

LINYPHIIDAE: This group is almost exclusively a climax inhabitant, though the data of table I do not show this fact too well. Their webs are very delicate and complex and are used for long periods if not destroyed by outside agencies (Emerton, '02). Wind is probably a limiting factor in the distribution of this group. The spider spins its web among herbaceous plants to quite an extent. Any major air movement would readily displace the web which is so delicately constructed that even slight breezes may disturb it. Moisture plays a role in restricting their distribution, as they are small spiders which probably could not tolerate much drying. The excessively moist woods at Smith contain all but one of the species which have been found in the dune areas, while the other climax areas have fewer species, which would indicate that moisture as great as that at Smith is of importance.

LYCOSIDAE: Most of the lycosids are free-running ground-inhabiting species without any permanent home. The various species show different reactions to temperature and moisture. Therefore, this family is widely distributed among the various associates. Due to their roving habits and their different reactions to temperature, moisture, light, etc., their distribution is rather more widespread than is that of other spiders. The beach and climax show the greatest variety of species. The beach, with its temporary

fauna of insects in the drift line, probably is the reason why there is a larger number of lycosids in this area. The cottonwood and pine show the least number of species, probably as much due to the lack of leaf mold in which they might hide during the day, as to the slight amount of moisture. In other words, the lack of cover and moisture in the first four associates is overcome by the roving tendencies of the species which come to the beach during the night to feed. In addition, some of the individuals are on the beach because they have been blown there—this is the case with the immature specimens. Beginning with the beach, there is, first of all, the species *Arctosa littoralis* which is found on the river margin sand areas and lake sand areas in the eastern and central states. These individuals hide during the day and come out to feed at night. These spiders whose gray color matches that of the sand almost exactly (especially by moonlight), indicate an interesting problem in protective coloration. The fore-dune and cottonwood dune species is *Geolycosa wrightii*; its one to two foot deep burrows are most common in these associates. There is no common or typical species in the pine dune. There are more species in the oak dune than in the climax forest. Further collecting of ground floor material will probably yield many more species. Moisture preferences and toleration experiments are needed to obtain solutions to the problems of distribution for this family. Trees or bushes and even herbaceous plants are virtually of no significance as substrata for this group. Sweeping of vegetation yields only an occasional specimen (Lowrie, '42).

MICRYPHANTIDAE: The distribution of the members of the family Micryphantidae, due to incomplete collecting, probably has no significance in this study. They are a minute species requiring special collecting techniques not used sufficiently in the present work to give a clear picture of their distribution. One species, *Ceraticelus emertoni*, is found commonly in the herb stratum of the black oak dune (Lowrie, '42). However, the climax for-

est will probably yield the majority of species, as the micryphantids are largely leaf mold inhabitants.

MIMETIDAE: This family is too rare for any exact analysis. They are probably climax forms, as shown by their distribution and the fact that the species are easily killed by desiccation.

OXYOPIDAE: The one species of lynx spider in this area is largely characteristic of open woods or grasslands. It is a diurnal species found roving about on the grasses of the black oak dunes.

PISAURIDAE: The members of this family are diverse in habit for such a small group. In general, they require much moisture (some species will die in a dry container within four hours), while *Pissaurina mira* may be found in dry, open oak dunes. *Dolomedes triton sexpunctatus* is found only in or on ponds or streams so perhaps it should be excluded from this study, as it is not particularly characteristic of any one stage. In general, the family is more common in climax areas than in earlier stages, though the species may be fewer.

SALTICIDAE: Generalizations about this family are made only with hesitation, as the family is so large and diverse. Weese ('24) has shown *Metaphidippus capitatus* (*galathea* or *protervus*) to be quite tolerant of dry air (evaporation of 2.2 to 2.8 cc. per hour) which might account for its wider distribution. *Pellenes agilis*, *Pellenes borealis*, *Metaphidippus galathea*, *Phidippus clarus*, *Phidippus insignarius*, and *Maevia vittata* are the only species common in the early associates. All but *Pellenes borealis* are also to be found in later associates and are fairly common throughout the succession. A few more species appear in the pine dune, and still more in the black oak dune, where they reach their greatest abundance. The reduction in the herbaceous stratum in the climax forest is probably responsible for the reduction in number of climax salticids as these spiders are largely herbaceous stratum species. Over half the species in the family have been collected by

sweeping, and all the common species were found in the herbaceous layer.

THERIDIIDAE: Like the linyphiids, this family is more abundant in the climax than elsewhere. Only five species, *Latrodectus mactans*, *Lithyphantes albomaculatus*, *Steatoda borealis*, *Theridion differens* and *Theridion murarium*, are found in numbers, except in the climax. *Latrodectus mactans* in the Chicago region is a pine, black oak and oak-hickory associates species. It has never been found in deep moist woods. *Lithyphantes albomaculatus* is possibly even more of a dry open land species as it is found in the cottonwood zone as well. *Steatoda borealis* is a wide-ranging species extending into the climax. *Theridion murarium* may be a typical pine species, as it has been collected in the pine associates on many occasions and in great numbers on the branches among the pine needles. The remaining species are almost entirely climax forms, though several are found in the black oak as well. Substratum and evaporation are of importance here for these species are web-builders.

THOMISIDAE: Most of the crab spiders are found on herbaceous plants—as shown by sweeping—and on tree trunks. Many of the species are yellow and match the flowers in which they hide and catch their prey. Others are brown and gray, similar to the bark of trees on and under which they hide. Of special interest is *Philodromus alascensis* which has been found in greatest abundance on the fore-dune and cottonwood dune. Its presence here was explained earlier. Members of the genus *Ebo* also are characteristic fore-dune, pine, and oak species, being found on the grasses in these associates. *Philodromus aureolus* is the only species of crab spider which seems to be widespread. Species of the genus *Xysticus* are more characteristic of the climax and black oak associates, where they are found on the bark of trees to a great extent. Therefore, substratum is of importance for this group as well as for the web-builders.

ULOBORIDAE: The two members of the family Uloboridae found in the Chicago

region are undoubtedly climax forms, or, at least, forms requiring as much moisture as is found in the climax. Their small soft bodies seem to be readily desiccated; efforts to keep them alive in the laboratory meet with little success, unless the jars in which they are kept contain water. Substratum is also important, for their webs are found strung between trees or stout branches. Temperature, as is true for many others discussed, must also be important as they are both more common in the southern United States.

ORDER ARANEIDA

In summing up the distribution of spiders in general, the following facts are to be considered. No single family, not even of the larger ones, shows close correspondence with each associates. In other words, each family may be divided into two or, at most, five or six different categories overlapping the plant associates. Considering the order as a whole, however, there are finer distinctions which give evidence for dividing the succession into at least six categories. The last two will be likely to show characteristic species when further work is done. Table III gives a listing of the typical species of each associates as shown by this study. The physical factors of importance are the following. Substratum is of importance for support of webs and as additional area on which to roam and in the form of leaf mold for ground level inhabitants. Moisture is also important; several species have been shown to require a certain amount of moisture; others, such as *Latrodectus mactans*, are not common in moist areas, if found at all. Temperature is of importance, as it is to any invertebrate. The strength of the wind is undoubtedly of importance to web builders whose webs would be destroyed by too powerful a wind. Light also affects the spiders, primarily in regard to their day-night distribution, and secondarily by the effect of the heat and evaporation. Biotic factors are also important in that the plants provide changes in the physical factors which have been listed above and

TABLE III. *Characteristic spiders of the dune associates*

| | |
|--------------------|---|
| Beach | <i>Arctosa littoralis</i> , lycosids in general. |
| Foredune | <i>Philodromus alascensis</i> , <i>Pellenes borealis</i> , <i>Dictyna bostoniensis</i> , <i>Geolycosa wrightii</i> . |
| Cottonwood | <i>Geolycosa wrightii</i> , <i>Dictyna bostoniensis</i> , <i>Philodromus alascensis</i> , <i>Pellenes borealis</i> . |
| Pine | <i>Theridion murarium</i> , <i>Mangora gibberosa</i> , <i>Dictyna foliacea</i> , <i>Ceraticelus fissiceps</i> , <i>Dictyna frondea</i> . |
| Black Oak | Many species; Vagabond species (lycosids, salticids, thomisids, etc.) predominant. |
| Subclimax | Transitional forms—many climax forms appear, such as <i>Uloborus americana</i> . |
| Beech-maple climax | Web-builders (especially linyphiids). |
| Ubiquitous species | <i>Eustala anastera</i> , <i>Tetragnatha laboriosa</i> , <i>Schizocosa avida</i> , <i>Metaphidippus galathea</i> , <i>Philodromus aureolus</i> , <i>Neoscona arabesca</i> , <i>Clubiona obesa</i> , <i>Pellenes agilis</i> , <i>Phidippus clarus</i> , <i>Phidippus insignarius</i> . |

also because the insects and other small terrestrial invertebrates increase greatly as the climax is reached, so there is more food to support a larger spider population.

QUANTITATIVE ANALYSIS OF THE HERBACEOUS STRATUM IN THE VARIOUS ASSOCIATES

A comparative analysis of the herbaceous stratum in the various associates was attempted during the latter part of August 1940 and during 1941. The areas collected were Ogden Dunes, Dune Acres and Smith, Indiana. Specimens from one hundred sweeps with a heavy duty sweeping net of approximately twelve inches in diameter were placed together in a vial and later identified. These one hundred sweep units were then totalled as presented in table IV. Unfortunately, it was impossible to make an equal number of sweeps in each of the areas, so the results are not strictly comparable quantitatively. The number of sweeps in the cottonwood, subclimax and climax areas are too small for any conclusions to be drawn, except that the species collected

are found in the respective areas. Probably the only area which was swept enough for quantitative comparison was the black oak dune. The percentage of non-web-builders and the density of population vary too greatly to show any accurate picture.

The relative abundance of the various species, however, is of some value as it is a basis for conclusions drawn as to the character of the spider population. This has already been discussed in the earlier summaries of the species of the various associates. However, one additional fact may be noted in this regard. The abundance

of spiders as a group in the herbaceous layers of each of the associates is indicated by the number of sweeps necessary to collect one specimen in each associate (table IV). The average of 2.7 sweeps to capture one spider, and the fact that all but cottonwood and pine collections approach the average closely, indicates that vegetation of the herbaceous layer tends to support the same number of spiders in the area of the study regardless of the associates in which the stratum is located. The large number of sweeps necessary to collect one specimen in the pine and especially in the cottonwood is

TABLE IV. *Quantitative analysis of the herbaceous stratum*
SW—Number of 100-sweep units in which species was collected.
S—Number of specimens collected.

| Species | Fore-dune | | Cotton-wood | | Pine | | Oak | | Sub-climax | | Climax | |
|---------------------------------|-----------|----|-------------|---|------|----|-----|-----|------------|----|--------|------------|
| | SW | S | SW | S | SW | S | SW | S | SW | S | SW | S |
| <i>Agelenopsis</i> sp. im. | | | | | | | | | 1 | 1 | | |
| <i>Acanthepeira stellata</i> | 1 | 1 | | | | | | | | | | |
| <i>Aranea thaddeus</i> | | | | | | | 4 | 5 | | | | |
| <i>Aranea raji</i> | | | | | | | | | | | 1 | 1 |
| <i>Argiope aurantia</i> | 1 | 1 | | | | | 2 | 2 | | | | |
| <i>Argiope trifasciata</i> | | | | | | | 6 | 7 | | | | |
| <i>Eustala anastera</i> | 1 | 1 | 1 | 1 | | | 5 | 9 | 1 | 1 | 1 | 1 |
| <i>Leucauge venusta</i> | | | | | 1 | 1 | 4 | 4 | 4 | 13 | | |
| <i>Mangora gibberosa</i> | | | | | 2 | 4 | 11 | 58 | | | | |
| <i>Mangora maculata</i> | | | | | | | | | 3 | 6 | 1 | 1 |
| <i>Micrathena sagittata</i> | | | | | | | 2 | 2 | 1 | 1 | | |
| <i>Neoscona arabesca</i> | 1 | 1 | 1 | 2 | 2 | 3 | 9 | 26 | | | 1 | 1 |
| <i>Tetragnatha laboriosa</i> | 5 | 10 | 2 | 4 | 5 | 13 | 14 | 69 | | | 3 | 4 |
| Immature argiopids | | | | | 1 | 1 | | | 1 | 1 | | |
| <i>Dictyna bostoniensis</i> | 4 | 10 | 1 | 1 | | | | | | | | |
| <i>Dictyna foliacea</i> | | | | | 3 | 3 | 1 | 1 | 2 | 11 | | |
| <i>Dictyna frondea</i> | | | | | 1 | 1 | 8 | 18 | | | | |
| <i>Dictyna volucris</i> | | | | | | | 2 | 2 | | | | |
| Immature <i>Dictynas</i> | | | | | 1 | 1 | 3 | 3 | | | | |
| <i>Ceraticelus emertoni</i> | | | | | | | 14 | 49 | | | 1 | 2 |
| <i>Ceraticelus fissiceps</i> | | | | | 3 | 10 | | | 1 | 1 | | |
| Immature micryphantids | 1 | 1 | | | 1 | 2 | 4 | 4 | | | 2 | 4 |
| Immature <i>Mimetus</i> sp. | | | | | | | | | 2 | 4 | 1 | 2 |
| <i>Latrodectus mactans</i> | | | | | 1 | 1 | 2 | 2 | | | | |
| <i>Theridion differens</i> | | | | | 1 | 2 | 13 | 33 | 2 | 2 | | |
| <i>Theridion frondeum</i> | | | | | | | 3 | 6 | 4 | 5 | 2 | 6 |
| <i>Theridion murarium</i> | | | | | 4 | 9 | | | 1 | 1 | | |
| <i>Ulesanis americana</i> | | | | | | | | | | | 1 | 1 |
| Immature theridiid | | | | | | | | | 1 | 1 | | |
| <i>Bathypantes formica</i> | 1 | 1 | | | | | 1 | 1 | | | | |
| <i>Linyphia maculata</i> | | | | | | | | | | | 1 | 1 |
| <i>Linyphia pusilla</i> | | | | | | | 1 | 1 | | | | |
| Immature <i>Linyphia</i> sp. | | | | | | | 1 | 1 | | | 1 | 1 |
| <i>Pityohyphantes phrygiana</i> | | | | | | | | | 2 | 5 | | |
| <i>Uloborus americana</i> | | | | | | | | | 1 | 1 | 2 | 3 |
| Total web-builders | 15 | 26 | 5 | 8 | 26 | 51 | 109 | 302 | 27 | 60 | 18 | 48 200 495 |

TABLE IV—Continued

| Species | Fore-dune | | Cotton-wood | | Pine | | Oak | | Sub-climax | | Climax | | | |
|-------------------------------------|-----------|-----|-------------|----|------|-----|------|-----|------------|-----|--------|-----|------|------|
| | SW | S | SW | S | SW | S | SW | S | SW | S | SW | S | SW | S |
| <i>Aysa gracilis</i> | | | | | | | 3 | 6 | | | 3 | 33 | | |
| <i>Anyphaena celer</i> | | | | | | | | | 1 | 1 | | | | |
| Immature <i>Agroeca</i> sp. | | | | | | | 1 | 1 | | | | | | |
| Immature <i>Clubiona</i> sp. | 1 | 2 | | | 1 | 1 | 10 | 16 | 1 | 1 | | | | |
| <i>Micaria aurata</i> | | | | | | | 1 | 1 | | | | | | |
| <i>Micaria</i> sp. | | | | | | | 1 | 1 | | | | | | |
| <i>Trachelas tranquillus</i> | | | | | | | 1 | 1 | | | | | | |
| Immature sp. of <i>Gnaphosid</i> | | | | | | | | | 1 | 1 | | | | |
| <i>Lycosa rabida</i> | | | | | | | 1 | 1 | | | 2 | 4 | | |
| <i>Oxyopes salticus</i> | | | | | | | 1 | 1 | | | | | | |
| Immature <i>Dolomedes</i> sp. | | | | | | | 1 | 2 | 1 | 1 | 3 | 11 | | |
| <i>Pisaurina mira</i> | | | | | | | 2 | 4 | 1 | 1 | | | | |
| <i>Evarcha hoyi</i> | | | | | | | 1 | 1 | | | | | | |
| <i>Hentzia mitrata</i> | | | | | | | 7 | 7 | 2 | 6 | 2 | 4 | | |
| <i>Maevia vittata</i> | | | | | 4 | 34 | 22 | 211 | 2 | 2 | 2 | 2 | | |
| <i>Metaphidippus galathea</i> | 1 | 2 | | | 6 | 32 | 5 | 9 | 3 | 6 | 3 | 21 | | |
| Im. <i>Metaphidippus</i> sp. | | | | | | | | | 1 | 2 | | | | |
| <i>Paraphidippus marginatus</i> | | | | | 5 | 23 | | | 2 | 15 | 2 | 2 | | |
| <i>Pellenes agilis</i> | | | | | 4 | 10 | 10 | 24 | | | | | | |
| <i>Pellenes arizoniensis</i> | | | | | 1 | 1 | | | | | | | | |
| <i>Pellenes borealis</i> | 6 | 19 | 1 | 4 | 1 | 2 | | | | | | | | |
| <i>Pellenes calcaratus</i> | | | | | | | 1 | 1 | | | | | | |
| <i>Phidippus clarus</i> | | | | | | | 5 | 10 | 1 | 1 | | | | |
| <i>Phidippus insignarius</i> | 1 | 2 | 1 | 1 | 4 | 7 | 12 | 46 | | | | | | |
| Immature sp. <i>Phidippus</i> | | | | | | | | | | | 1 | 3 | | |
| <i>Tutelina elegans</i> | | | | | | | 5 | 14 | | | | | | |
| Immature <i>Zygoballus</i> sp. | 1 | 1 | | | | | | | | | | | | |
| Immature salticid | 2 | 3 | | | | | 1 | 1 | | | | | | |
| <i>Misumenoides aleatorius</i> | | | | | 1 | 2 | 7 | 10 | | | | | | |
| <i>Misumenops asperatus</i> | | | | | 1 | 2 | 9 | 28 | 1 | 1 | 3 | 10 | | |
| Immature <i>Misumenops</i> sp. | | | | | 1 | 1 | 10 | 20 | | | | | | |
| <i>Misumenops oblongus</i> | | | | | 1 | 3 | | | | | | | | |
| <i>Philodromus alascensis</i> | 8 | 75 | 2 | 8 | 1 | 1 | | | | | | | | |
| <i>Philodromus aureolus</i> | | | | | 5 | 17 | 7 | 25 | | | | | | |
| <i>Philodromus ornatus</i> | | | | | | | | | | | 2 | 2 | | |
| <i>Philodromus pernix</i> | | | | | 1 | 1 | 2 | 2 | | | | | | |
| Immature <i>Philodromus</i> sp. | | | | | | | 1 | 1 | | | | | | |
| Immature <i>Thanatus</i> sp. | | | 1 | 1 | | | 1 | 1 | | | | | | |
| <i>Tmarus angulatus</i> | | | | | | | | | 1 | 1 | | | | |
| <i>Tibellus oblongus</i> | | | | | | | 2 | 4 | | | | | | |
| <i>Xysticus banksi</i> | | | | | | | | | 1 | 1 | | | | |
| <i>Xysticus fraternus</i> | | | | | 1 | 1 | 15 | 50 | 3 | 4 | 2 | 2 | | |
| Immature <i>Xysticus</i> sp. | | | | | | | 1 | 1 | | | | | | |
| Total non-web-builders | 20 | 104 | 5 | 14 | 38 | 138 | 148 | 502 | 21 | 43 | 26 | 97 | 258 | 898 |
| Total number of specimens | 35 | 130 | 10 | 22 | 64 | 189 | 257 | 804 | 48 | 103 | 44 | 145 | 458 | 1393 |
| Per cent of non-web-builders | 57 | 80 | 50 | 64 | 59 | 73 | 58 | 62 | 44 | 42 | 59 | 67 | 57 | 65 |
| Number of sweeps | 800 | | 200 | | 900 | | 2300 | | 300 | | 300 | | 4800 | |
| Average number of sweeps per spider | 2.7 | | 9.1 | | 4.8 | | 2.9 | | 2.9 | | 2.1 | | 2.7 | |

probably an expression of the more sparse condition of the herbaceous stratum. Obviously, much more work must be done before definite proof of these observations is obtained.

SUMMARY

1. Two hundred and twenty-eight species of spiders found in the dunes along

the southern shore of Lake Michigan, and in the black oak and foredune areas of Kankakee and Waukegan, are listed according to the associates in which they have been collected.

2. The physical and biotic factors have been noted and their possible effects on the spiders considered.

3. Seventeen species of spiders were found on the beach which has a population of predominantly free-running forms, of which *Arctosa littoralis* is the most common.

4. Thirty-one species were found in the foredune of which four are characteristic, *Philodromus alascensis* being most typical as it builds a retreat in the foredune grasses.

5. Eighteen species were found on the cottonwood dune though more were probably there. The same four species are characteristic of this stage as are characteristic of the preceding associates. This associates does not seem to be distinct from the foredune as far as the spiders are concerned.

6. Forty-three species are found in the pine dune, and at least five of them are characteristic. More protected, less rigorous conditions with greater variety of habitats are probably the causes of this increase in number of species.

7. One hundred and sixty-eight species are found in the black oak, fifty-six in the subclimax and one hundred twenty-two in the climax.

8. The apparent large number of species in the climax, proportionately to the black oak dune, is probably due to the lack of a large climax forest. A typical form readily enters most parts of the small beech-maple woods investigated.

9. An average of about two and one-half sweeps is necessary to collect one spider in the herbaceous stratum.

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LIFE-FORM SPECTRA OF THE HARDWOOD FORESTS OF THE ITASCA PARK REGION, MINNESOTA

MURRAY F. BUELL

Rutgers University, New Brunswick, N. J.

ROBERT L. WILBUR

University of Hawaii, Honolulu

The principal objective of this paper is to present a comparison of the life-form spectra of the climax community as it occurs at the climatic margin of the deciduous forest formation with similar spectra obtained from the formation nearer its climatic optimum. This is done with Raunkiaer's thesis in mind, that there is a progressive change in the life-form spectrum as one moves away from warm, humid climates to colder or drier climates. He showed that, as the more severe climate is approached, life-form spectra based upon floras of different regions show an increasing emphasis on those species whose perennating buds lie near or within the ground (Raunkiaer, '34). His life-form classes are used here. The spectra are based upon the species of the climax community only.

Data were obtained during August of 1946 and 1947 on ten hardwood forest stands near the University of Minnesota Biological Station at Itasca Park, Minnesota. The stands chosen are distributed over an area extending from Ponemah, on the Red Lakes Peninsula in Beltrami County seventy miles north of Itasca Park, to central Becker County thirty miles southwest of Itasca Park. To the west the area extends to the eastern edge of Norman County about fifty miles west of Itasca Park.

Five stands occur at or near the prairie margin while the others lie well back from it. Although the latter are in a region mapped by Upham (1884) as conifer forest, they are actually within a broad tension zone between the northern conifers and the deciduous forest (fig. 1) (Buell and Gordon, '45). The limit drawn by Upham represents approximately the western boundary of this tension zone. In contrast, the transition be-

tween forest and prairie at this latitude is often exceedingly abrupt. Three of the stands are right next to such an abrupt margin, another lies in a forest peninsula extending into prairie, while the fifth is in the midst of the hardwood forest band.

The objective in selecting stands was to find a relatively undisturbed representative hardwood forest along the prairie margin and in the hardwood-conifer tension zone. None of the stands found was without some minor human interference but those used represent about as satisfactory samples as can be found in the area.

METHODS

Frequency data were obtained for the tree, shrub and herb layers of each of the ten stands by the following procedure: Ten sets of quadrats were located at ten meter intervals through the forest. The presence of mature trees was determined on 10×10 meter quadrats, and saplings and shrubs were listed from a 2×8 meter plot within each of the larger quadrats. Herbs were listed from four $\frac{1}{4} \times 4$ meter quadrats located at the corners of the tree plots. Thus the list of herbs is based on areas of 40 square meters, shrubs on 160 square meters and trees on 1000 square meters in each stand. In the tabulation, the four herb plots located in each tree plot were included as a unit resulting in ten units of four square meters each per stand.

The terms frequency and constancy are not used in the strictly conventional sense in this paper. Frequency is a value usually applied to the concrete, individual stand. As used here it refers to the total number of quadrats in which a species occurred. Since ten quadrats were used in each of the ten stands this total num-

ber of quadrats is 100. Frequency is expressed as per cent and since 100 quadrats were used the frequency and the number of quadrats in which the species occurred are the same. Constancy is presence on a unit area basis. Actually the "unit area" used here is the total area of the ten quadrats in each stand. This "unit area" thus differs for the tree, shrub, and herb layers as indicated in the above paragraph. A constancy of ten, for example, indicates that a species occurred in the plots at least once in all ten stands.

Frequency points are used in some of the spectra presented in the results of this study. The usual life-form spectrum is based upon the species list, or in other words, the mere presence of the species in the community. The chance occurrence of one plant of a species thus gives that species the same importance in the usual life-form spectrum as have those

species which contribute most to the vegetation. Frequency points for a life-form as used here refer to the sum of the frequencies of the various species representing that life-form. For instance in the total of 100 quadrats of the ten stands, *Carex pennsylvanica* occurs in 94. Since it is a cryptophyte it contributes 94 frequency points, while *Clintonia borealis*, which occurs in three quadrats, contributes three frequency points to the total frequency of cryptophytes. Since larger quadrats were used to sample the shrub and tree layers, the phanerophytes are not included in the frequency point spectra.

Assignment of the species to a life-form has been made primarily with reference to McDonald's ('37) study of the life-forms of Indiana. However, some species as they grow in the hardwood forests of northern Minnesota assume a different life-form. Thus, in several instances, the

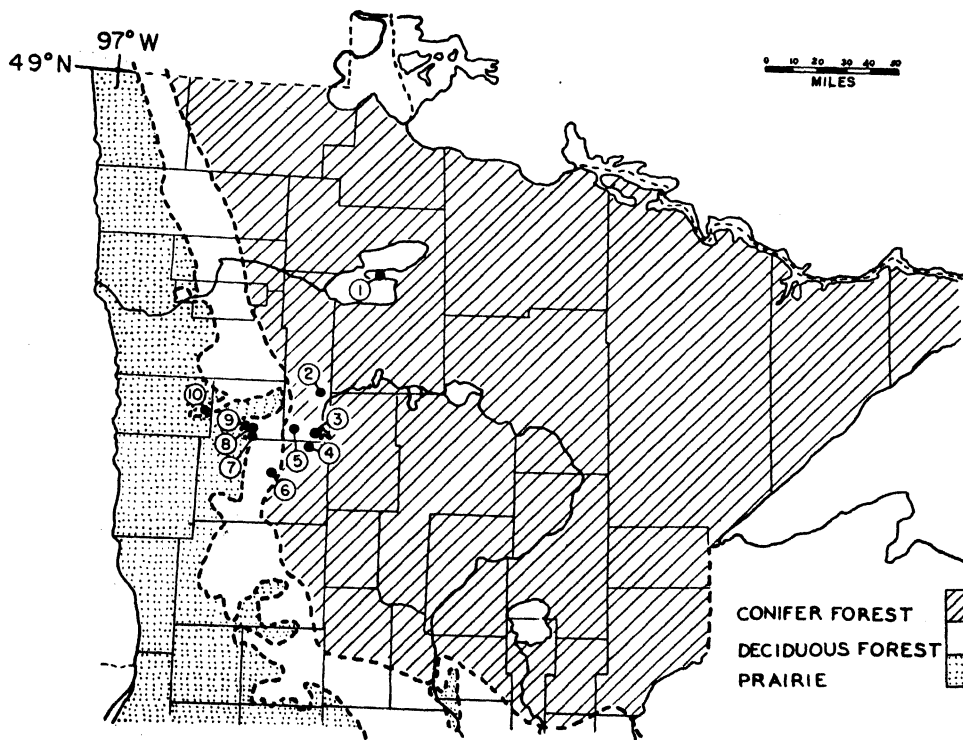


FIG. 1. Map of northern Minnesota redrawn from vegetational map of Minnesota in *Trees and shrubs of Minnesota* by Rosendahl and Butters, originally made by Upham in 1884. Location of the ten stands is shown by the numbers.

TABLE 1. Constancy and frequency chart of species¹ occurring on plots included in the study; constancy class values: 1 = species occurring in 81-100% of the stands, 2 = spp. in 61-80%, 3 = spp. in 41-60%, 4 = spp. in 21-40%, 5 = spp. in less than 21%. C (constancy) values = number of stands in which the species occurred in one or more of the quadrats; F (frequency) values = per cent of the quadrats in which the species was found.

| Constancy class | Phanerophytes | | Chamaephytes | | Hemicryptophytes | | Cryptophytes | |
|-----------------|---|---|--|--------------|---|---|--|----------------------------------|
| | Species | C-F | Species | C-F | Species | C-F | Species | C-F |
| 1 | <i>Tilia americana</i> <i>Quercus macrocarpa</i> var. <i>olivaeformis</i> <i>Acer saccharum</i> <i>Ostrya virginiana</i> <i>Prunus virginiana</i> | 10-85 10-50 9-75 9-75 9-45 | | | <i>Thalictrum dioicum</i> <i>Aralia nudicaulis</i> <i>Viola pubescens</i> <i>Gallium triflorum</i> | 10-74 10-60 10-25 9-44 | <i>Carex pennsylvanica</i> <i>Oakeia sessilifolia</i> <i>Uvularia grandiflora</i> <i>Oryzopsis asperifolia</i> | 10-94 10-63 9-83 9-62 |
| 2 | <i>Corylus rostrata</i> <i>Ulmus americana</i> <i>Quercus borealis</i> var. <i>maxima</i> <i>Viburnum affine</i> var. <i>hybomalacum</i> <i>Populus tremuloides</i> <i>Betula papyrifera</i> | 8-52 8-42 8-38 8-28 7-32 7-16 | | | <i>Aster macrophyllus</i> <i>Solidago flexicaulis</i> <i>Maianthemum canadense</i> <i>Sanicula marilandica</i> <i>Lathyrus ochroleucus</i> <i>Rubus pubescens</i> Raf. <i>Osmorhiza claytoni</i> <i>Viola blanda</i> | 8-48 8-38 8-29 7-29 7-25 7-22 7-19 7-12 | <i>Streptopus longipes</i> <i>Anemone quinquefolia</i> | 7-23 7-21 |
| 3 | <i>Celastrus scandens</i> <i>Ribes cynosbati</i> <i>Fraxinus pennsylvanica</i> and var. <i>lanceolata</i> <i>Fraxinus nigra</i> <i>Amelanchier humilis</i> <i>Cornus alternifolia</i> | 6-24 6-24 6-23 5-18 5-12 5-12 | <i>Lonicera dioica</i> var. <i>glaucescens</i> <i>Parthenocissus vitacea</i> | 6-11 6-11 | <i>Asarum canadense</i> <i>Amphicarpa monoica</i> <i>Hepatica americana</i> (DC) Ker. <i>Phryma leptostachya</i> | 6-24 6-21 5-36 5-14 | <i>Smilacina racemosa</i> | 6-20 |
| 4 | <i>Acer spicatum</i> <i>Abies balsamea</i> <i>Dirca palustris</i> <i>Ulmus fulva</i> <i>Ribes iris</i> <i>Rubus strigosus</i> <i>Cornus rugosa</i> <i>Lonicera canadensis</i> <i>Rosa blanda</i> <i>Carpinus caroliniana</i> | 4-24 4-21 4-19 4-12 4-9 4-5 3-11 3-9 3-7 3-4 | <i>Rhus toxicodendron</i> | 4-22 | <i>Fragaria virginiana</i> <i>Hystrix patula</i> <i>Pyrola elliptica</i> <i>Aquilegia canadensis</i> <i>Rudbeckia laciniata</i> <i>Aster lindleyanus</i> <i>Aralia racemosa</i> <i>Solidago serotina</i> <i>Mitella nuda</i> <i>Zizia aurea</i> <i>Desmodium grandiflorum</i> | 4-13 4-10 4-7 4-5 3-18 3-12 3-11 3-10 3-8 3-8 3-6 | <i>Circaea alpina</i> <i>Adiantum rubra</i> <i>Botrychium virginianum</i> <i>Sanguinaria canadensis</i> <i>Dryopteris spinulosa</i> (Muell.) Watt | 4-8 4-6 4-4 3-15 3-3 |

¹ *Carex pedunculata* is omitted since it was overlooked in the work done in 1946. It would be in constancy class 1 and would have a fairly high frequency as indicated by results from two stands included from work done in 1947.

TABLE I—Continued

| Constancy class | Planerophytes | | Chamaephytes | | Hemicryptophytes | | Cryptophytes | |
|-----------------|------------------------------------|------|---------------------------------|-----|-----------------------------------|-----|-----------------------------------|------|
| | Species | C-F | Species | C-F | Species | C-F | Species | C-F |
| 5 | <i>Corylus americana</i> | 2-13 | <i>Lycopodium obscurum</i> var. | 1-3 | <i>Lucula campestris</i> | 2-9 | <i>Arisaema triphyllum</i> | 2-10 |
| | <i>Acer rubrum</i> | 2-10 | <i>dendroideum</i> (Michx.) | | <i>Smilax herbacea</i> | 2-9 | <i>Oryzopsis racemosa</i> | 2-8 |
| | <i>Pinus strobus</i> | 2-5 | Eaton | 1-1 | <i>Elymus canadensis</i> | 2-8 | <i>Caulophyllum thalictroides</i> | 2-4 |
| | <i>Picea canadensis</i> | 2-4 | <i>Ribes prostratum</i> | | <i>Thalictrum dasycarpum</i> | 2-7 | <i>Clintonia borealis</i> | 2-3 |
| | <i>Symphoricarpos albus</i> | 2-4 | | | <i>Pyrola asarifolia</i> | 2-5 | <i>Pteridium aquilinum</i> var. | 2-3 |
| | <i>Crataegus rotundifolia</i> var. | 2-4 | | | <i>Aster lateriflorus</i> | 2-8 | <i>latiusculum</i> (Desv.) | |
| | <i>pubera</i> | | | | <i>Bromus purgans</i> | 2-3 | Underw. | |
| | <i>Crataegus punctata</i> | 2-3 | | | <i>Galium boreale</i> | 2-3 | <i>Carex gracillima</i> | 2-2 |
| | <i>Populus grandidentata</i> | 2-3 | | | <i>Lathyrus venosus</i> | 2-3 | <i>Circaea intermedia</i> | 2-2 |
| | <i>Diervilla lonicera</i> | 2-2 | | | <i>Muhlenbergia</i> sp. | 2-3 | <i>Helianthus divaricatus</i> | 1-7 |
| | <i>Prunus nigra</i> | 2-2 | | | <i>Prenanthes alba</i> | 2-3 | <i>Athyrium angustum</i> | 1-3 |
| | <i>Sambucus pubens</i> | 2-2 | | | <i>Solidago canadensis</i> | 2-2 | (Willd.) Presl. | |
| | <i>Symphoricarpos occidentalis</i> | 1-10 | | | <i>Sonchus arvensis</i> | 2-2 | <i>Pteritis pennsylvanica</i> | 1-2 |
| | <i>Taxus canadensis</i> | 1-9 | | | <i>Urtica gracilis</i> | 2-2 | (Willd.) Fern. | |
| | <i>Viburnum trilobum</i> | 1-7 | | | <i>Viola conspersa</i> | 1-6 | <i>Trillium grandiflorum</i> | 1-2 |
| | <i>Zanthoxylum americanum</i> | 1-7 | | | <i>Festuca nutans</i> | 1-4 | <i>Veronicastrum virginicum</i> | 1-2 |
| | <i>Cornus candidissima</i> | 1-5 | | | <i>Taraxacum</i> sp. | 1-3 | (L.) Farwell | |
| | <i>Viburnum lentago</i> | 1-5 | | | <i>Aster paniculatus</i> | 1-2 | <i>Cirsium arvense</i> | 1-1 |
| | <i>Vitis vulpina</i> | 1-5 | | | <i>Cornus canadensis</i> | 1-2 | <i>Cypripedium</i> sp. | 1-1 |
| | <i>Acer negundo</i> | 1-4 | | | <i>Cryptolaenia canadensis</i> | 1-2 | <i>Habenaria hyperborea</i> | 1-1 |
| | <i>Ribes americanum</i> | 1-4 | | | <i>Lactuca</i> sp. | 1-2 | <i>Heracleum lanatum</i> | 1-1 |
| | <i>Clematis virginiana</i> | 1-2 | | | <i>Agastache anthiodora</i> | 1-1 | <i>Humulus lupulus</i> | 1-1 |
| | <i>Prunus serotina</i> | 1-2 | | | (Nutt.) Britton | | <i>Smilactina stellata</i> | 1-1 |
| | <i>Populus balsamifera</i> | 1-1 | | | <i>Astragalus canadensis</i> | 1-1 | | |
| | <i>Quercus ellipsoidalis</i> | 1-1 | | | <i>Bromus ciliatus</i> | 1-1 | | |
| | <i>Ulmus racemosa</i> | 1-1 | | | <i>Cinna latifolia</i> | 1-1 | | |
| | | | | | <i>Erigeron philadelphicus</i> | 1-1 | | |
| | | | | | <i>Geum strictum</i> | 1-1 | | |
| | | | | | <i>Heuchera richardsonii</i> var. | 1-1 | | |
| | | | | | <i>hispidior</i> R.B.L. | | | |
| | | | | | <i>Nepeta cataria</i> | 1-1 | | |
| | | | | | <i>Oxalis stricta</i> | 1-1 | | |
| | | | | | <i>Plantago rugelii</i> | 1-1 | | |
| | | | | | <i>Pyrola secunda</i> | 1-1 | | |
| | | | | | <i>Schizachne purpurascens</i> | 1-1 | | |
| | | | | | (Torr.) Swallen | | | |
| | | | | | <i>Splenopholis intermedia</i> | 1-1 | | |
| | | | | | Rydb. | | | |
| | | | | | <i>Trientalis americana</i> | 1-1 | | |
| | | | | | <i>Triosteum perfoliatum</i> | 1-1 | | |
| | | | | | <i>Vicia americana</i> | 1-1 | | |

assignment of plants to life-form categories differs from the Indiana list. This includes the vines—*Rhus toxicodendron*, *Lonicera dioica*, *Parthenocissus vitacea* and *Lonicera hirsuta*. They persist only as chamaephytes, their perennating buds being limited to the portion of the shoot that remains near the ground.

The names of the phanerophytes and chamaephytes are those used by Rosendahl and Butters ('28). The rest follow the nomenclature of Gray's Manual, 7th Ed. (Robinson and Fernald, '08) with the few exceptions where the authority is given following the name.

RESULTS

The floristic composition of the forests and some idea of the contribution of the various species can be derived from table I which shows both constancy and frequency data. Three tree species, *Tilia americana*, *Acer saccharum*, and *Quercus macrocarpa* var. *olivaeformis*, all having both high constancy and frequency, characterize the community. *Ostrya virginiana* is the main understory tree; *Prunus virginiana* and *Corylus rostrata* the principal shrubs; no chamaephytes play a conspicu-

ous role in the forests. Among the herbs, the hemicryptophytes present a larger total number than the cryptophytes, and therophytes are not represented at all. Among the hemicryptophytes *Thalictrum dioicum*, *Aralia nudicaulis*, *Aster macrophyllus*, and *Viola pubescens* are the most important. Among the cryptophytes *Carex pennsylvanica*, which is essentially ubiquitous, *Oakesia sessilifolia*, *Uvularia grandiflora* and *Oryzopsis asperifolia* are very high in both constancy and frequency.

The life-form spectra based upon the flora of the stands reveal differences both within the region and between the Itasca region and other parts of the eastern deciduous forest. Within the Itasca Park area there is an appreciable change in life-form spectra along an east-west line. This is evident when the two spectra in table II, Section A, are compared. The spectrum constructed from the species list of the five prairie margin stands shows a small but consistent shift to the right, i.e., toward the more protected life-form classes, when compared with the spectrum derived from the species list of the five stands in the conifer-hardwood forest tension zone.

TABLE II. Life-form spectra based on species lists: A. from two groups of hardwood forest stands in the Itasca region; B. from the ten Minnesota stands included in A, compared with those of a similar study on the North Carolina Piedmont. The arrows point direction of shift in emphasis when the second spectrum of each group is compared with the one just above it.

| | Number of species | Life-forms | | | | |
|--|-------------------|------------|-----|------|------|----|
| | | Ph | Ch | H | Cr | Th |
| <i>Per cent</i> | | | | | | |
| A Flora of 5 Minnesota hardwood forest stands in conifer-hardwood forest tension zone | 91 | 38.5 | 4.4 | 41.7 | 15.4 | 0 |
| Flora of 5 Minnesota hardwood forest stands along prairie margin | 125 | 35.2 | 3.2 | 45.6 | 16.0 | 0 |
| <i>Per cent</i> | | | | | | |
| B North Carolina Piedmont Climax by Oosting, 1942 | 89 | 59.6 | 0 | 36.0 | 4.5 | 0 |
| Minnesota hardwoods, 10 stands ² | 145 | 35.9 | 2.8 | 44.1 | 17.2 | 0 |

² Pteridophytes are not included; with them included the spectrum is: Ph = 34.4, Ch = 3.4, H = 42.3, Cr = 19.9, Th = 0.

TABLE III. *Climatic data for Mahnomen^a and Itasca Park; data from Climatic Summary of the United States, Section 44, 1930*

| | J | F | M | A | M | J | J | A | S | O | N | D | Annual |
|---------------------------|-------|------|------|------|------|------|------|------|------|------|------|------|--------|
| Precipitation (inches) | | | | | | | | | | | | | |
| Mahnomen (19 yrs.) | .35 | .33 | .80 | 1.57 | 2.80 | 2.89 | 3.41 | 3.03 | 2.48 | 1.59 | .82 | .57 | 20.64 |
| Itasca Park (20 yrs.) | .66 | .67 | .85 | 1.74 | 3.26 | 4.09 | 2.87 | 3.37 | 2.48 | 1.78 | .98 | .88 | 23.63 |
| Average Snowfall (inches) | | | | | | | | | | | | | |
| Mahnomen (11 yrs.) | 5.4 | 3.3 | 6.0 | 4.6 | .7 | 0 | 0 | 0 | T | .8 | 5.9 | 8.4 | 35.1 |
| Itasca Park (18 yrs.) | 7.6 | 6.6 | 7.3 | 1.4 | .4 | 0 | 0 | 0 | T | 2.0 | 3.6 | 9.4 | 38.3 |
| Average Min. Temp. (°F.) | | | | | | | | | | | | | |
| Mahnomen (12 yrs.) | -9.0 | -3.6 | 14.9 | 28.0 | 40.4 | 50.1 | 54.3 | 52.4 | 42.9 | 33.5 | 17.1 | 3.5 | 27.3 |
| Itasca Park (19 yrs.) | -10.5 | -4.2 | 8.8 | 27.2 | 37.2 | 47.8 | 52.3 | 49.1 | 42.1 | 30.2 | 17.6 | .4 | 24.8 |
| Average Max. Temp. (°F.) | | | | | | | | | | | | | |
| Mahnomen (12 yrs.) | 13.5 | 18.3 | 35.3 | 51.9 | 66.1 | 74.5 | 80.2 | 78.4 | 68.7 | 55.2 | 35.5 | 22.0 | 50.0 |
| Itasca Park (19 yrs.) | 15.4 | 21.6 | 35.4 | 53.1 | 66.7 | 74.7 | 79.6 | 76.8 | 67.5 | 56.3 | 37.9 | 20.9 | 50.5 |

^a Mahnomen data are combined with some from Beaulieu, 8 miles to the east.

The magnitude of the climatic difference involved, as recorded by meteorological instruments, can be seen through inspection of table III. The records of two Weather Bureau stations, one in Itasca Park, the other at Mahnomen, are compared. The Itasca Park station is in the conifer-hardwood forest tension zone, while Mahnomen is along the prairie margin. On the map (fig. 1) Mahnomen is just northwest of stand 9 while the Itasca Park records were taken just northeast of stand 3. From the table it can be seen that Mahnomen receives 2.99 inches less precipitation annually than the Itasca station. During the growing season—May through August—Mahnomen receives 1.46 inches less rainfall. The snowfall at Mahnomen averages 3.2 inches less. The figures for the average maximum and minimum temperatures show that Mahnomen has slightly higher average monthly minimum temperatures than Itasca but the latter has higher maximum temperatures except for the late summer months of July, August, and September. The prairie margin, then, is more xeric as evidenced by the lower summer rainfall and lower winter precipitation. Its summers are hotter. Its winter protection of snow cover is less. Altogether it has a more rigorous climate for plants than that of the conifer-hardwood forest tension zone.

In table II B is a spectrum based on the species list obtained in sampling all ten hardwood stands compared with one obtained from a similar study of the climax hardwood forests of the North Carolina Piedmont in autumnal aspect (Oosting, '42). Both this Itasca spectrum and one by Daubenmire ('36) for the central Minnesota "Big Woods" show a pronounced shift in the emphasis toward the right (toward the more protected life-form classes) when compared with the North Carolina spectrum. Although these differences are probably real, the effect may possibly be due to the difference in the season of sampling. There is practically a reversal, however, when one compares the Minnesota spectra with spectra based on the flora of the mixed mesophytic forest (Withrow, '32) and the cove hardwoods (Cain, '45). In both of these latter, the very much more numerous cryptophytic element and the presence of therophytes shift the emphasis to the right end of the spectrum as compared with the Minnesota spectrum. This is not what one would be led to expect on the basis of Raunkiaer's thesis, i.e. a shift to emphasis on the more protected forms as colder and drier conditions are approached.

The use of frequency points instead of the species list, however, has very different results. Such use of frequency points for

constructing life-form spectra places the spectrum on an entirely different basis. Species as such are essentially disregarded and frequency of recurrence of a life-form as represented by the species is considered. As far as it is applicable, it is more significant ecologically than basing spectra on the species list, for the emphasis is thus shifted from the floristic to the vegetational viewpoint. A few chance individuals of incidental species cannot effect such a spectrum very much compared with those which make an appreciable contribution to the community.

TABLE IV. *Life-form spectra showing, with the aid of arrows, the direction in which the emphasis shifts when frequency points rather than species lists are used as a basis*

| | Life-forms | | | |
|---|------------|------|------|-----|
| | Ch | H | Cr | T |
| Great Smokies Cove Hardwoods Cain, 1945 | | | | |
| | per cent | | | |
| 1. Species list | 6.6 | 61.3 | 29.3 | 2.6 |
| 2. Frequency points (aestival aspect) | 14.2 | 58.6 | 23.9 | 3.3 |
| North Carolina Pied- mont Climax (Autumnal aspect) Oosting, 1942 | | | | |
| 3. Species list | 0 | 88.9 | 11.1 | 0 |
| 4. Frequency points | 0 | 92.3 | 7.7 | 0 |
| Itasca region, 10 stands | | | | |
| 5. Species list | 4.3 | 68.8 | 26.9 | 0 |
| 6. Frequency Points | 3.6 | 60.4 | 36.0 | 0 |

Using frequency points, Cain ('45) constructed a spectrum for the cove hardwoods and compared it with the spectrum based upon the species list. We found a pronounced shift toward the less protected life-form classes when frequency points were used (table IV, lines 1 and 2). With data kindly furnished by Dr. Oosting, the present authors have made

a similar comparison between flora and frequency points in the climax forests of the North Carolina Piedmont (table IV, lines 3 and 4). Again it should be mentioned that Oosting's data were collected in the fall when evidence of some of the early season plants had disappeared, and because of that are not entirely representative of the forest flora, while in the Minnesota stands where the growing season is so much shorter the lists constitute a much more complete record. However, the comparison of the North Carolina spectra for flora and frequency points is interesting and probably of some significance. As with the cove hardwoods, the use of frequency points causes the shift in emphasis toward the less protected life-form classes. In contrast, the Itasca forests show the opposite. There the use of frequency points results in a distinct shift in emphasis toward the right with appreciable increase of cryptophytes (table IV, lines 5 and 6).

A comparison of the frequency point life-form spectrum of the cove hardwoods and that of the Itasca hardwoods shows that the use of frequency points is especially desirable when two communities are being compared (table IV, lines 2 and 6). Here the Itasca hardwoods are represented by a greater emphasis on the right end of the spectrum than the cove hardwoods which lie at the center of the eastern deciduous forest. This is not true when the species list is used, as can be seen by lines 1 and 5, table IV, and as has already been discussed above.

There is also a pronounced difference between the hardwood forest at its dry climatic limit in Minnesota and its cold but moist climatic limit in eastern Canada. Dansereau ('43) has published a spectrum for the Laurentian region which shows a lower proportion of phanerophytes than in Minnesota but a corresponding gain in chamaephytes and hemicytrophytes. Certain conclusions can be drawn from the results of this study. In the first place in northern Minnesota the life-form spectrum of the climax forest changes rapidly

as its prairie limit is reached, the change being a shift toward emphasis on the more protected life-form classes. Furthermore, when frequency points are used there is a difference consistent for all life-forms between the spectrum of the climax community near the center of the deciduous forest formation and that at the prairie margin. This difference is such that it falls in nicely with Raunkiaer's thesis (Raunkiaer, '34). That this does not show up when the species list alone is used suggests the importance of using quantitative data as a basis for comparing life-form spectra of similar communities in different regions.

SUMMARY

1. Ten hardwood forest stands in the vicinity of Itasca Park, Minnesota, were sampled and species lists as well as frequency data were obtained for tree, shrub, and herb layers. The forests studied are characterized in the tree layer by a preponderance of *Tilia americana*, *Acer saccharum*, and *Quercus macrocarpa* var. *olivaeformis*.

2. Within the Itasca Park area the character of the flora of the hardwood forests changes along an east-west line, the effect of the prairie margin showing up in the comparison of spectra.

3. Results of comparing the northern Minnesota forests with the mixed mesophytic forest suggest that the species list is not a satisfactory basis on which to build life-form spectra in such a community comparison.

4. Spectra based upon frequency points are distinctly different from those based on species lists both in the climax forests of the Carolina Piedmont and the mixed mesophytic forests on the one hand and the Minnesota forests on the other. In

the former the use of frequency points shifts the emphasis to the less protected life-form classes, while in the forests of the Itasca Park region the emphasis shifts in the other direction. The result is such that, through the medium of frequency point spectra, the Minnesota forests do show the influence of the drier, more continental climate when compared with the mixed mesophytic forests of the southern Appalachians, as well as with the climax forests of the Carolina Piedmont.

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TOLERATION OF LOWERED OXYGEN TENSION BY CAVE AND STREAM CRAYFISH¹

W. D. BURBANCK, JOHN P. EDWARDS, AND MADELINE P. BURBANCK

Department of Biology, Drury College, Springfield, Missouri

Over a period of years it has been found that pond crayfish are more tolerant of lowered oxygen tension than are stream crayfish (Park, Gregg, and Lutherman, '40). Since there are many caves in Missouri inhabited by blind crayfish, it was thought that there might be similar physiological adaptations to environment and differences in toleration of crayfish living within caves as compared with those which occur in streams outside caves.

The cave selected for most intensive study lies in Christian County southeast of Springfield, Missouri and is known locally as Smallin's Cave. Alternate spellings which appear on maps of the region and with pictures of the cave are "Smallin" and "Smallen." Located on a branch of Finley Creek which is a tributary of the James River, the cave was partially explored by Henry R. Schoolcraft and three companions in 1819 and descriptions were subsequently published by Schoolcraft in 1821 and 1853 (Shepard, '98). His party was not able to penetrate the cave to any appreciable distance because at a point where it was about ten feet in width the stream of water occupied the whole passage and "the water, being dammed up below by a stalactitic incrustation deposited from it, forms a small lake in the bottom of the cave." The "lake" appeared to be ten or fifteen feet deep, "and the singular calcareous formation by which it is encompassed, gives it the appearance of a stupendous vase, or bath" (Schoolcraft, 1821). No animals were reported by Schoolcraft nor any name given to the cave. This cave is undoubtedly the one referred to by Broadhead ('74) in a geological survey of the state

of Missouri where he gives the following description:

"There are several caves near Ozark, Christian County, which issue from the same formations as those in Greene county. On a branch of Finley Creek a stream disappears in a sink, appearing again three quarters of a mile southeast through an opening 60 feet high by 98 feet wide. Up stream the cave continues this size for a hundred yards and then decreases in size, and for the next quarter of a mile further it is generally 10 by 14 feet wide. A very clear, cool stream passes out in which by careful search crawfish without eyes can be found."

The wide mouth of Smallin's Cave has been pictured in articles on Missouri caves (Shepard, '98; Simpich, '23; "White River country of Missouri"). One of the best views is that shown in figure 1 which was taken by the late Dr. James E. Cribbs while chairman of the Department of Biology, Drury College. Although the location appears on maps of the region, the cave has not been commercialized.

Cave animals and in particular cave crayfish have been reported from other caves of southern Missouri, but the reference by Broadhead ('74) to "crawfish without eyes" is the only published report on the fauna of Smallin's Cave which has been found. Garman ('89) reported on animals collected by Miss Ruth Hoppin from Wilson's cave and other caves and wells in Jasper County near Joplin, Missouri. The crayfish collected were sent to Prof. Walter Faxon for identification and subsequently described as a new species, *Cambarus setosus* Faxon. Both Garman ('99) and Faxon ('90) mention Broadhead's report of blind crayfish, and Faxon suggests that they are probably *C. setosus*. Another investigator of the caves of southwest Missouri was Carl H. Eigenmann. He visited caves in Stone, Barry, Jasper and Greene counties and

¹ We wish to thank Mr. Roy J. Myklebust for the preparation and standardization of reagents used in the Winkler analyses for dissolved oxygen during the 1946 experiment.

collected salamanders from Wilson's cave and from Fisher's cave near Springfield ('99 and '02). Although Eigenmann does not mention crayfish, Miss Mary I. Steele ('02) reports blind crayfish from both the Jasper County caves and wells and from Fisher's cave near Springfield, Missouri. Those from the latter locality were collected by Dr. Howard Ayers in 1897 and described as a new species, *Cambarus ayersii*, by Miss Steele. The animals resembled *C. setosus* but seemed distinct enough to warrant placing them in a new species. No subsequent report on cave crayfishes of southwest Missouri has been found other than a reference to *C. setosus* by Ortmann ('05) in a paper on the dispersal of *Cambarus* over the United States.

MATERIALS AND METHODS

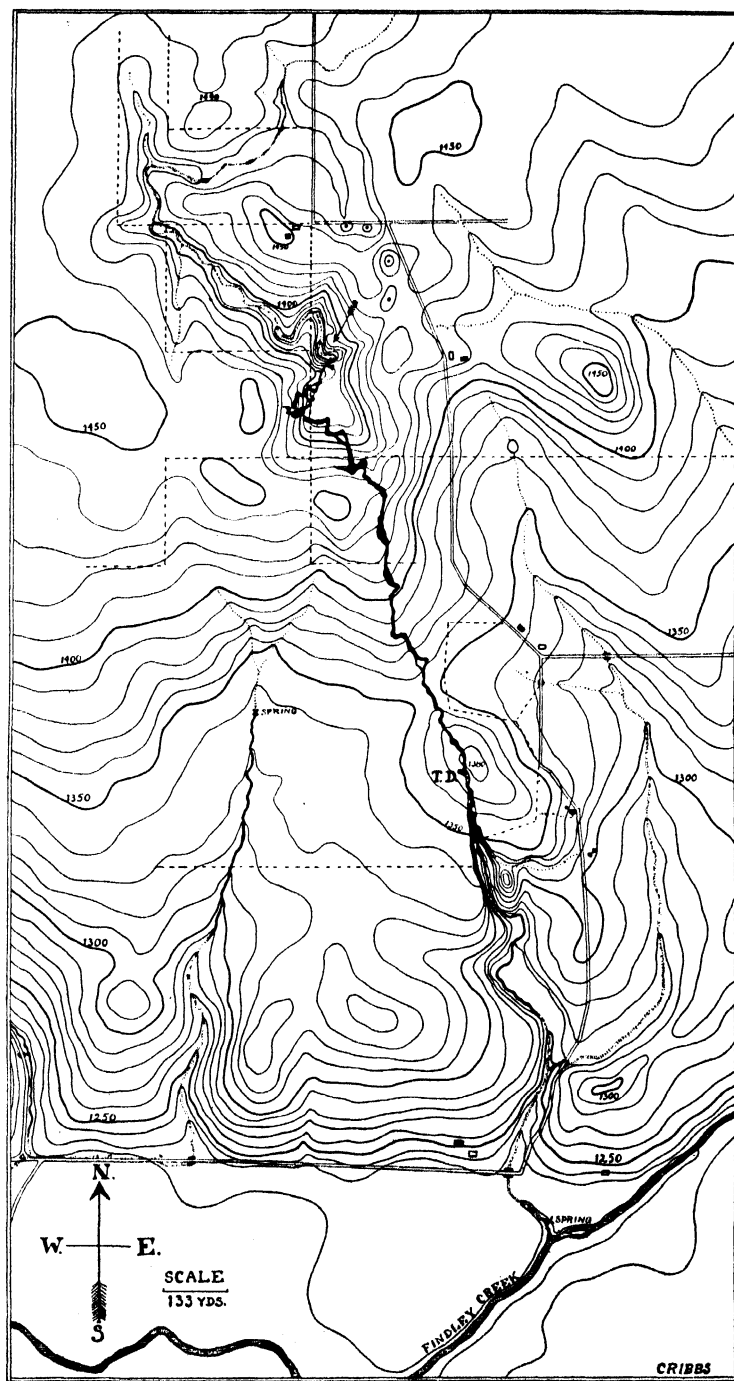
The cave crayfish for these oxygen tension experiments were collected from the stream within Smallin's Cave from the point of total darkness to a distance of about one-half a mile or as far as could be penetrated without crawling. The

point of total darkness (T. D., fig. 2), about 450 feet from the mouth of the cave, occurs about 150 feet beyond the vase formation described by Schoolcraft which can be scaled on foot when the water in the stream is not excessively high. Collections were made in June, 1946, and April and June, 1947 with the aid of a carbide lamp and flashlights. The animals collected appear to be *C. setosus* Faxon but show some characteristics of *C. ayersii* Steele and specimens have been sent to the National Museum in Washington for positive identification (Museum Reference No. 173686). Crayfish collected from the stream outside Smallin's Cave were used for the experiment performed in June, 1946. No crayfish could be found in this same stream in April, 1947. On his map of Smallin's Cave (fig. 2) Dr. Cribbs indicated that the flow of water in the stream a short distance outside Smallin's Cave was intermittent. A severe drought during the winter of 1946-47 caused parts of this stream to dry up completely. It is supposed that the stream crayfish either died or moved



(Photograph by J. E. Cribbs.)

FIG. 1. Mouth of Smallin's Cave as viewed from within.



LEGEND

- ROADS
- PRIVATE DRIVEWAY
- DRY STREAM BED
- CONTOUR LINE
- FENCE
- PATH TO CAVE
- HEAD OF CAVE
- FLOWING STREAM
- ⊙ SINK
- x SPRING

(Map by J. E. Cribbs.)

FIG. 2. Map of Smalin's Cave showing the topography of the surrounding territory.

downstream to deeper water and had not yet returned by June. Crayfish of the same species, *C. rusticus* Girard (Turner, '26), were collected from another tributary of Finley Creek about two miles distant which likewise issues from a cave. This cave, known as Wood Cave, is small and at the time collections were made the water was too high to permit penetration into the cave. A white "cave crayfish" was found at the mouth of the cave, however, so that conditions appeared similar enough to justify using cave specimens from Smallin's Cave and stream specimens from the stream outside Wood Cave for the experiments in April and June, 1947. The temperature of the water of the two streams was the same, 16° C., and subsequent statistical tests of the experimental results show that there is no significant difference between the survival times of the crayfish collected from the two different streams ($P = .4244$) (Simpson and Roe, '39); consequently, the data on stream crayfish from the stream flowing from Smallin's Cave (Exp. 1) and those taken from the stream issuing from Wood Cave (Exps. 2 and 3) were combined and treated as one when experimental results were summarized.

Oxygen tests such as those described by Park, Gregg and Lutherman ('40) were performed on a total of thirty-three stream and thirty-three cave crayfish in a series of three experiments which were

performed in June 1946 (Exp. 1), April 1947 (Exp. 2), and June 1947 (Exp. 3). The animals were used the day after they were collected. Three crayfish were placed in each experimental flask in boiled, cooled water collected from the mouth of Smallin's Cave, and the animals distributed in such a way that the biomass (total living weight) of each flask was approximately the same. The number of flasks per experiment was limited by the number of cave crayfish collected, e.g., three flasks of cave and three flasks of stream crayfish in Experiment 1, five of each in Experiment 2, and three of each in Experiment 3. Immobility was taken to be the death point.

RESULTS AND DISCUSSION

The results of the three experiments are summarized in table 1. In each experiment the cave crayfish survived longer than did the stream animals. Comparison of the mean survival times shows great similarity among the three experiments. In Experiment 1, the average cave crayfish lived 591.7 minutes longer than the average stream crayfish, in Experiment 2, 589.0 minutes longer, and in Experiment 3, 702.1 minutes longer. The greater difference in Experiment 3 occurs because the stream crayfish of this experiment were much shorter-lived than stream animals of the other experiments. The maximum-minimum range for the stream animals of Experiment 3 was 250-91 minutes

TABLE I. *Results of oxygen toleration tests*

| Habitat | Exp. | Number and sex | | Total weight (gms.) | Av. wt. per flask (gms.) | Oxygen tension, cc. per liter | | Mean survival time in order of death (min.) | | | Mean of means \pm P.E. (min.) | n - 1 |
|---------|------|----------------|---|---------------------|--------------------------|-------------------------------|-------|---|-------|--------|---------------------------------|-------|
| | | M | F | | | Start | End | 1 | 2 | 3 | | |
| Stream | 1 | 3 | 6 | 39.5 | 13.2 | 3.9844 | .0548 | 139.3 | 259.3 | 274.7 | 224.4 \pm 17.0 | 8 |
| | 2 | 8 | 7 | 68.3 | 13.7 | 3.9715 | .2956 | 327.0 | 368.6 | 451.0 | 382.2 \pm 19.6 | 14 |
| | 3 | 4 | 5 | 87.3 | 29.1 | 4.2587 | .2914 | 95.0 | 132.7 | 184.0 | 137.2 \pm 12.5 | 8 |
| Cave | 1 | 2 | 7 | 38.5 | 12.8 | 3.9844 | .0541 | 628.0 | 848.3 | 972.0 | 816.1 \pm 31.9 | 8 |
| | 2 | 8 | 7 | 69.3 | 13.7 | 3.9715 | .2885 | 753.2 | 964.4 | 1195.8 | 971.2 \pm 56.1 | 14 |
| | 3 | 2 | 7 | 79.0 | 26.3 | 4.2587 | .2323 | 644.0 | 841.0 | 1033.0 | 839.3 \pm 52.8 | 8 |

TABLE II. Summary of three oxygen toleration tests

| Habitat | Oxygen tension, cc. per liter | | Survival range (min.) | | Mean survival time in order of death (min.) | | | Mean of means \pm P.E. (min.) | Stan. Dev. | Coefficient of variability (%) | n - 1 |
|---------|----------------------------------|-------|--------------------------|------|--|-------|--------|---------------------------------------|---------------|---|-------|
| | Start | End | Min. | Max. | 1 | 2 | 3 | | | | |
| Stream | 4.0715 | .2453 | 91 | 501 | 212.5 | 274.5 | 330.1 | 272.3 ± 21.5 | 100.8 | 37.0 | 10 |
| Cave | 4.0715 | .1978 | 394 | 1585 | 689.3 | 899.1 | 1090.4 | 892.9 ± 35.0 | 163.9 | 18.4 | 10 |

while the range for all thirty-three stream crayfish used in the three experiments was 501-91 minutes. No unusual conditions of the natural stream habitat were observed at the time of collection which would account for the lowered survival rate of these stream crayfish.

When the data from the three experiments are combined it is seen that the average cave crayfish survived 620.6 minutes longer than the average stream crayfish (table II). This is a significant difference when tested by statistical methods ($P = 0.0000$). The death-order data of table II are shown graphically in figure 3. As in the pond-stream experiments reported by Park ('45), there is an increased divergence between survival times. The first stream crayfish to die in a flask succumbed on the average 476.8 minutes before the first cave crayfish. The average time of death of the second stream crayfish in each flask was 624.6 minutes before the second cave crayfish, and the average time of death for the third stream crayfish was 760.3 minutes before the death of the third cave crayfish. The cave crayfish of these experiments show greater survival ability in the presence of reduced oxygen when compared with stream forms than do the pond crayfish compared with stream forms as reported by Park ('45). Table II and figure 3 show that there is no overlap but rather a lapse of 359.2 minutes between the average time of death of the last stream crayfish and the average time of death of the first cave crayfish to die in each experimental flask (average based on 11 flasks). In the pond-stream work (Park, '45) where there were four animals in each experimental flask, the first

pond crayfish died on an average of 55.4 minutes before the last stream crayfish became immobile.

It is interesting to note (fig. 3) that once the initial death occurs in a flask the average lapse of time until the death of the second cave crayfish and of the second stream crayfish is 19 per cent of

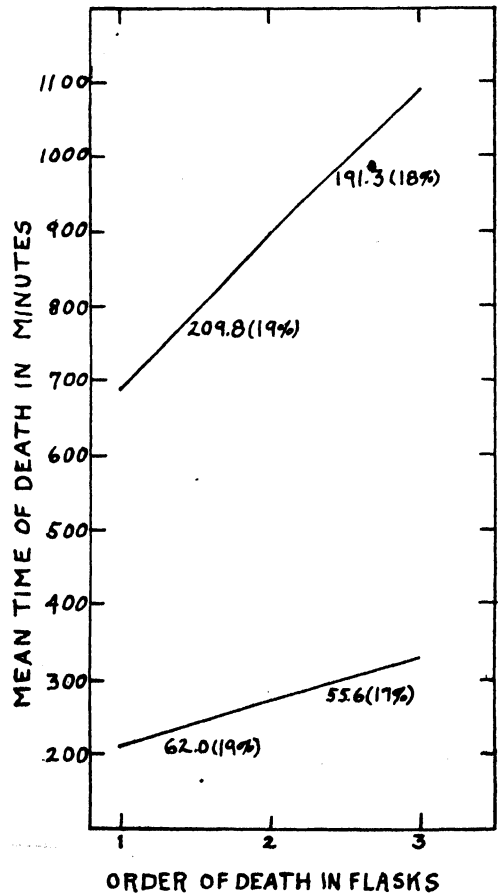


FIG. 3. Death-order of cave and stream crayfish plotted against survival time in water of reduced oxygen content.

the total average time between the beginning of the experiment and the death of the last crayfish in each set of experiments. Similarly the 55.6 minutes which elapse between the death of the second and third stream crayfish is 17 per cent of the average total time lapse of 330.1 minutes, while the 191.3 minutes between the second and third cave crayfish is 18 per cent of the average total time lapse of 1090.4 minutes. Thus, although the cave crayfish live longer, once the critical oxygen tension is reached, both cave and stream crayfish die at an equal rate.

There seems to be no correlation between size and survival time nor between sex and survival time of the cave and stream crayfish. There was a tendency for the smaller cave crayfish to be shorter-lived than the medium-sized or large-sized animals, but there was no similar tendency among the stream crayfish. The cave crayfish ranged in size from 1.2 gm. to 15.0 gm. and the stream crayfish from 1.5 gm. to 15.2 gm. The two longest-lived cave crayfish were a female weighing 5.8 gm. which survived 1585 minutes and a male weighing 6.5 gm. which survived 1580 minutes. These animals were together in one flask of Experiment 2. The two shortest-lived cave crayfish were one in Experiment 3 which was a female, weighed 2.5 gm. and lived 394 minutes, and a female in Experiment 1 which weighed 1.5 gm. and lived 473 minutes.

Winkler analyses of the oxygen content of the experimental flasks at the beginning of each experiment and after the death of the last animal show that the oxygen was reduced by about the same amount by both cave and stream animals (table I). In each experiment the cave animals reduced the oxygen content to a slightly greater extent than did the stream crayfish, but there is no statistical difference ($P = .3596$) between .2452 and .1978, the figures which appear in table II as the average oxygen tensions of the water in the stream and cave flasks at the end of the experiments. This final result differs from the data reported by

Park ('45) where the longer-lived pond crayfish reduced the oxygen to a greater extent than did the stream crayfish. Thus for the pond-stream experiments the conclusion is reached that the pond crayfish are more tolerant of lowered oxygen content of water since they live longer than do the stream crayfish and in water with a lower oxygen content. The cave crayfish, however, lived longer than did the stream crayfish, but the oxygen tension of the water was not reduced appreciably below that of the water which contained stream crayfish. The cave crayfish, then, cannot be said to tolerate a lower oxygen tension than that for stream crayfish but may have a lower metabolic rate which reduced the oxygen content of the water more slowly. The cave crayfish appear rather sluggish in their movements and tolerate each other to a greater extent than do the stream crayfish. Cave animals will kill weakened cave crayfish but do not fight among themselves as do the stream crayfish when under crowded conditions. A study of the accumulation of carbon dioxide or other waste products and the source of food of the cave crayfish would be of value in analyzing further the apparent difference in rate of metabolism.

The results of these experiments indicate that cave crayfish are able either to live longer in water with a reduced oxygen content than are stream crayfish or to reduce the oxygen content at a slower rate. There is, then, a physiological adjustment to environment by these cave crayfish in addition to the external physical changes of white coloration, eyelessness, and long antennae typical of cave forms. These physiological adjustments may be directly related to differences in physical environment. Stream crayfish can seek deeper water downstream during dry weather and may benefit from oxygen produced by the aquatic plants which occur outside but not inside the cave, but the cave crayfish are limited to the kind and amount of water which is in the cave.

Analysis of the oxygen content of the water outside and inside Smallin's Cave² shows that the oxygen content is variable but averages about the same. The temperature of water in the stream outside the cave and within the cave has been found to be always the same. Temperature and oxygen content are thus eliminated as causative environmental factors which might influence animals in the two habitats. Cave water is usually low in organic material as compared with streams in which water plants grow and into which animal and vegetable debris may fall. Smallin's Cave is unique, however, in this respect since the sink hole opening allows a considerable quantity of organic matter in the form of soil, leaves and twigs to be washed into the cave. The cave crayfish are found in pools in which such sediment has accumulated.

The amount of water in Smallin's Cave varies greatly and is related directly to the moisture conditions of the surrounding territory. Following a prolonged dry spell late in the summer of 1946, the stream within but near the mouth of the cave was reduced to a few shallow pools. The larger pools immediately above and below the vase formation contained water but at a considerably lower level than had existed in the spring. When some rain did fall the stream flowed again, and after several days of almost continuous rain late in October the stream in Smallin's Cave was a small torrent with water several inches deep across the whole width of the cave almost to the mouth. The blind crayfish are not usually found in the semi-dark region of the cave, but on one occasion white crayfish were seen in a pool in this region. The stream was flowing at the time but the amount of water was not excessive.³ Following a

prolonged drought early in 1947, the stream outside Smallin's Cave was almost completely dried up and within the cave, both in the semi-dark and completely dark regions, the stream was reduced to pools with no water flowing between. Blind crayfish were observed in such pools in the dark regions. It must be borne in mind, therefore, that the crayfish of Smallin's Cave, although limited spatially by the confines of the cave, seem to be able to adapt themselves to great variations in water volume. Their habitat may be variously classified as a pond, as a slow-moving stream with much of the water supplied by seepage along the course of the stream, and as a rushing current of fast-moving water.

It is not known whether it is possible for the crayfish of Smallin's Cave to migrate from the cave itself to other underground water. Blind crayfish have been reported from deep wells in Missouri (Steele, '02; Garman, '89). Whether they breed there or migrated to the wells is not known. During the present study of Smallin's Cave, although more female than male animals have been collected, no females carrying eggs nor any very young crayfish have been collected. The life cycle of these cave crayfish remains unknown.

Further experiments are expected to be undertaken on ecological conditions in Smallin's Cave and might well be undertaken on other caves of Missouri and in other parts of the country where cave species of *Cambarus* are known to occur. It must be remembered that such experiments which by their very nature necessitate the death of the experimental animals must not be carried out on such a large scale as to deplete to extinction or near-extinction the population of the cave being studied.

SUMMARY

Smallin's Cave in Christian County, Missouri, is peculiar in two ways. First, the mouth of the cave is one of the largest in the United States, measuring about

² Private communication from Mr. Roy J. Myklebust.

³ We wish to thank Mrs. Evelyn Chaffin Pronko for observations of conditions in the cave during the fall of 1946 which she made in connection with weekly visits to the cave for experimental purposes of her own.

ninety-eight feet wide by sixty feet high. Secondly, in the space of three-quarters of a mile, the cave tapers to less than ten feet and opens into a deep sinkhole, a condition allowing much organic material in the form of leaves and soil to enter the cave.

In Smallin's Cave is found the white, blind crayfish, *Cambarus setosus*. Directly outside the cave and living under practically the same conditions of temperature, dissolved oxygen, pH, and total hardness of water, lives the stream crayfish, *Cambarus rusticus*. Since the surface drainage is a factor in the total flow of water in Smallin's Cave, the cave crayfish at times may live in a torrent, a swift stream, or in isolated ponds. During periods of drought the stream issuing from the cave may dry up and the stream crayfish disappear.

In a series of three experiments thirty-three stream and thirty-three cave crayfish were placed three each in liter flasks of boiled cooled water ($O_2 = 4.0715$) sealed with mineral oil. Following the death of all the animals oxygen analysis by the Winkler method showed that the cave and stream crayfish reduced the water to approximately the same oxygen tension—no significant difference between .1978 and .2452 respectively. The cave crayfish lived longer than did the stream crayfish, however. Average survival time for cave crayfish was 829.9 ± 35.0 minutes and for stream crayfish 272.3 ± 21.5 minutes. Thus the longer-lived cave crayfish seem to have a lower rate of metabolism than the stream crayfish.

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THE FECUNDITY AND DEVELOPMENT OF THE FLOUR BEETLES, *TRIBOLIUM CONFUSUM* AND *TRIBOLIUM* *CASTANEUM*, AT THREE CONSTANT TEMPERATURES¹

THOMAS PARK AND MARIAN BURTON FRANK

Hull Zoölogical Laboratory, The University of Chicago

Data have been accumulated on the fecundity and rate of development of the flour beetles *Tribolium confusum* and *Tribolium castaneum* at three constant temperatures as part of an extensive investigation of interspecies competition now under way in this laboratory. Because these data seem to have some utility in their own right, apart from the major program, they are summarized in this brief paper.

MATERIALS AND METHODS

Temperature and humidity control.—All determinations were carried out in incubators set to run at 24°, 29°, and 34° C. The actual performance of these three incubators is shown in table I from which it is apparent that the average temperatures maintained during the assay periods are close to the desired values. The variability, as indexed by the standard deviations, is similar for each chamber and the daily deviations above and below the mean were evenly distributed in time. The readings were taken inside each incubator but measurements showed the temperature of the medium was similar to that of the surrounding air.

An attempt was made to keep the relative humidity of each incubator within the range of 70 to 75 per cent. Table I suggests that this was accomplished moderately well and it seems reasonable to conclude that no important differentials in terms of *relative* humidity were established between the different cham-

bers. This, of course, does not hold for saturation deficit; these values increasing with temperature from 6.2 mm., to 7.5 mm., to 11.2 mm.

Techniques involved in the assay of fecundity.—Fecundity was measured by following the procedures outlined by Park and Davis ('45) which take advantage of the fact that infested flour can be screened through a bolting cloth sieve of such fine mesh that all eggs are retained for accurate counting.

One hundred and twenty shell vials were prepared by adding to each eight grams of a "standard laboratory medium" consisting of 95 per cent sifted whole-wheat flour and 5 per cent brewer's yeast powder. Forty of these vials were placed in the 24° incubator, 40 in the 29° incubator, and 40 in the 34° incubator. There they remained for six days in order to come into equilibrium with the obtaining temperatures and humidities, after which, one pair of beetles not exceeding two weeks of imaginal age was introduced into every vial. The replicates were evenly distributed so that, initially, there were 20 bottles containing *T. confusum* and 20 containing *T. castaneum* in each of the three temperature chambers.

After 72 hours, the beetles were gently removed and placed into vials with eight grams of fresh medium. The eggs were then counted and the numbers recorded vial-by-vial. This procedure was continued for the entire group of 120 samples for 10 egg censuses, or, until the rate of oviposition had been assayed for 30 days.

Techniques involved in the assay of rate of metamorphosis.—The objective was to determine the mean length of the egg, larval, and pupal stages of *Tribolium*

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TABLE I. *Mean temperatures and humidities maintained in the three incubators used in these experiments*

| | Temperature, ° C. | | Relative humidity | | Saturation deficit (mm.) | N |
|-----------------|-------------------|------|-------------------|------|--------------------------|----|
| | Mean \pm P.E. | S.D. | Mean \pm P.E. | S.D. | | |
| Incubator No. 1 | 23.98 \pm 0.06 | 0.72 | 75.56 \pm 0.35 | 3.98 | 6.2 | 59 |
| Incubator No. 2 | 29.06 \pm 0.08 | 0.68 | 75.10 \pm 0.70 | 5.75 | 7.5 | 31 |
| Incubator No. 3 | 33.99 \pm 0.09 | 0.65 | 71.88 \pm 0.59 | 4.12 | 11.2 | 22 |

TABLE II. *Oviposition rate per female per 72 hour interval of Tribolium confusum and Tribolium castaneum at temperatures of 24, 29, and 34° C.*

| Interval (days) | Mean \pm P.E. (eggs) | S.D. (eggs) | C.V. (%) | N | Interval (days) | Mean \pm P.E. (eggs) | S.D. (eggs) | C.V. (%) | N |
|-------------------------------------|------------------------|-------------|----------|-----|--------------------------------------|------------------------|-------------|----------|-----|
| <i>Tribolium confusum</i> at 24° C. | | | | | <i>Tribolium castaneum</i> at 24° C. | | | | |
| 0-3 | 10.8 \pm 0.36 | 2.4 | 22.2 | 20 | 0-3 | 17.4 \pm 0.68 | 4.5 | 25.9 | 20 |
| 3-6 | 15.2 \pm 0.63 | 4.2 | 27.6 | 20 | 3-6 | 22.5 \pm 0.69 | 4.6 | 20.4 | 20 |
| 6-9 | 17.2 \pm 0.63 | 4.2 | 24.4 | 20 | 6-9 | 21.2 \pm 1.13 | 7.5 | 35.4 | 20 |
| 9-12 | 15.9 \pm 0.93 | 6.2 | 39.0 | 20 | 9-12 | 18.6 \pm 1.34 | 8.9 | 47.8 | 20 |
| 12-15 | 16.1 \pm 0.87 | 5.8 | 36.0 | 20 | 12-15 | 19.3 \pm 1.13 | 7.5 | 38.9 | 20 |
| 15-18 | 16.1 \pm 0.79 | 5.1 | 31.7 | 19 | 15-18 | 18.2 \pm 1.24 | 8.2 | 45.0 | 20 |
| 18-21 | 14.2 \pm 0.79 | 5.1 | 35.9 | 19 | 18-21 | 19.3 \pm 1.16 | 7.7 | 39.9 | 20 |
| 21-24 | 14.5 \pm 0.94 | 6.1 | 42.1 | 19 | 21-24 | 17.8 \pm 1.21 | 8.0 | 44.9 | 20 |
| 24-27 | 13.0 \pm 0.97 | 6.3 | 48.5 | 19 | 24-27 | 18.3 \pm 1.02 | 6.8 | 37.2 | 20 |
| 27-30 | 13.7 \pm 1.02 | 6.6 | 48.2 | 19 | 27-30 | 18.0 \pm 1.09 | 7.2 | 40.0 | 20 |
| 0-30 | 14.7 \pm 0.27 | 5.6 | 38.1 | 195 | 0-30 | 19.1 \pm 0.35 | 7.3 | 38.2 | 200 |
| <i>Tribolium confusum</i> at 29° C. | | | | | <i>Tribolium castaneum</i> at 29° C. | | | | |
| 0-3 | 25.0 \pm 0.72 | 4.8 | 19.2 | 20 | 0-3 | 42.7 \pm 1.70 | 11.3 | 26.5 | 20 |
| 3-6 | 38.0 \pm 1.06 | 7.0 | 18.4 | 20 | 3-6 | 53.4 \pm 1.57 | 10.4 | 19.5 | 20 |
| 6-9 | 38.0 \pm 1.16 | 7.7 | 20.3 | 20 | 6-9 | 53.5 \pm 1.69 | 11.2 | 20.9 | 20 |
| 9-12 | 42.6 \pm 1.48 | 9.8 | 23.0 | 20 | 9-12 | 61.0 \pm 2.13 | 14.1 | 23.1 | 20 |
| 12-15 | 43.0 \pm 1.69 | 11.2 | 26.0 | 20 | 12-15 | 57.8 \pm 1.82 | 12.1 | 20.9 | 20 |
| 15-18 | 40.3 \pm 0.88 | 5.7 | 14.1 | 20 | 15-18 | 49.6 \pm 1.64 | 10.9 | 22.0 | 20 |
| 18-21 | 43.3 \pm 1.04 | 6.7 | 15.5 | 20 | 18-21 | 52.6 \pm 2.76 | 18.3 | 34.8 | 20 |
| 21-24 | 38.8 \pm 1.18 | 7.6 | 19.6 | 20 | 21-24 | 47.6 \pm 2.05 | 13.6 | 28.6 | 20 |
| 24-27 | 35.9 \pm 1.01 | 6.5 | 18.1 | 20 | 24-27 | 45.6 \pm 2.34 | 15.5 | 34.0 | 20 |
| 27-30 | 36.8 \pm 1.41 | 9.1 | 24.7 | 20 | 27-30 | 40.8 \pm 2.14 | 14.2 | 34.8 | 20 |
| 0-30 | 38.2 \pm 0.45 | 9.3 | 24.4 | 200 | 0-30 | 50.5 \pm 0.70 | 14.7 | 29.1 | 200 |
| <i>Tribolium confusum</i> at 34° C. | | | | | <i>Tribolium castaneum</i> at 34° C. | | | | |
| 0-3 | 32.9 \pm 1.45 | 9.4 | 28.6 | 20 | 0-3 | 43.9 \pm 1.81 | 11.7 | 26.6 | 19 |
| 3-6 | 42.5 \pm 1.19 | 7.7 | 18.1 | 20 | 3-6 | 63.1 \pm 2.23 | 14.8 | 23.4 | 20 |
| 6-9 | 43.6 \pm 1.44 | 9.3 | 21.3 | 20 | 6-9 | 58.6 \pm 2.07 | 13.7 | 23.4 | 20 |
| 9-12 | 49.7 \pm 1.38 | 8.9 | 17.9 | 20 | 9-12 | 64.6 \pm 1.64 | 10.9 | 16.9 | 20 |
| 12-15 | 48.0 \pm 1.58 | 10.2 | 21.2 | 20 | 12-15 | 63.9 \pm 1.66 | 11.0 | 17.2 | 20 |
| 15-18 | 44.7 \pm 1.21 | 7.8 | 17.4 | 19 | 15-18 | 55.9 \pm 1.86 | 12.0 | 21.5 | 19 |
| 18-21 | 46.0 \pm 1.33 | 8.6 | 18.7 | 19 | 18-21 | 58.7 \pm 2.09 | 13.5 | 23.0 | 19 |
| 21-24 | 41.9 \pm 1.93 | 12.5 | 29.8 | 19 | 21-24 | 56.4 \pm 1.67 | 10.8 | 19.1 | 19 |
| 24-27 | 41.3 \pm 1.92 | 12.4 | 30.0 | 19 | 24-27 | 57.6 \pm 1.67 | 10.8 | 18.7 | 19 |
| 27-30 | 36.5 \pm 2.26 | 14.6 | 40.0 | 19 | 27-30 | 48.5 \pm 2.40 | 15.5 | 32.0 | 19 |
| 0-30 | 42.7 \pm 0.56 | 11.4 | 26.7 | 195 | 0-30 | 57.2 \pm 0.68 | 14.0 | 24.5 | 194 |

confusum and *T. castaneum* at the three temperatures with a maximal range of error of ± 3 hours.

A mass culture consisting of several thousand *T. confusum* imagoes was established in a large jar containing fresh medium. After six hours, the newly laid eggs were collected and from this group three batches, each containing 56 eggs, were selected at random and placed into empty syracuse dishes. These dishes were put into the incubators at 24°, 29°, and 34°. Such a procedure initiates three cohorts whose later development can be followed and dated in terms of their individual members. As the first instar larvae emerge, the fact is noted and the elapsed time in hours between collecting the eggs and their hatching is taken as the duration of the egg stage. The larvae were then placed singly into vials containing two grams of medium and immediately returned to the respective temperatures at which they developed as eggs. These larvae were not disturbed until they had pupated, and the recording, by vials, of the time of pupation measures the length of the larval period for each larva. The pupal stage is timed in the same way, namely: the interval from pupation to eclosion is determined. Precisely similar procedures were followed simultaneously for *T. castaneum*.

The reduction in numbers within the N-columns of table V is accounted for by death of members of each cohort during larval development. It is evident that there was negligible mortality at the two lower temperatures for both species. At 34°, the mortality was higher, being approximately 20 per cent.

FECUNDITY

The data concerned with fecundity are presented in table II, that reports mean fecundity rate by intervals for both species of beetles at the three temperatures; in table III that compares selected mean differences in these rates in ratio to their probable errors, and in table IV, that shows the percentage differences in rates

both between species at the same temperatures and within species at different temperatures.

From these tables the following points are to be noted:

(1) Regardless of the temperatures involved, *T. castaneum* has a higher rate of oviposition than does *T. confusum*. This point has been suggested before on the basis of studies conducted at 29° (Park, '48; Park and Davis, '45) but it has not been proved up to this time by fecundity assays under identical conditions at a series of temperatures. Since the present data were collected under the favorable circumstances of no crowding, negligible egg cannibalism, renewed and nutritious medium, and a modicum of handling, it is reasonable to conclude that the rates reported are close to the maximum possible for the beetles maintained in the particular experimental conditions described. Further, it seems to follow that the difference between the two *Tribolium* is primarily a *species* difference which leads to the generalization that *T. castaneum* possesses an innately higher reproductive potential than does *T. confusum*.

The differences between the means for the entire period of study (0 to 30 day interval), when compared by species for each of the three temperatures, are all

TABLE III. Selected statistical comparisons of the oviposition rates for the 0-30 day interval reported in table II

| Comparison | Mean difference ± P.E. |
|---|---------------------------|
| <i>T. castaneum</i> - <i>T. confusum</i> , at 24° | 4.4±0.44 |
| <i>T. castaneum</i> - <i>T. confusum</i> , at 29° | 11.8±0.83 |
| <i>T. castaneum</i> - <i>T. confusum</i> , at 34° | 14.5±0.87 |
| <i>T. confusum</i> , 29°-24° | 24.0±0.52 |
| <i>T. confusum</i> , 34°-29° | 4.0±0.72 |
| <i>T. castaneum</i> , 29°-24° | 31.4±0.78 |
| <i>T. castaneum</i> , 34°-29° | 6.7±0.98 |

highly significant statistically as borne out in table III. These differences decrease with temperature: *T. castaneum* oviposits, on the average, 14.5 more eggs per female per 72 hours than does *T. confusum* at 34°; 11.8 more eggs at 29°, and 4.4

TABLE IV. Per cent that smaller oviposition rates are of larger oviposition rates (from the data reported in table II for the 0-30 day interval)

| The fraction | Quotient |
|---|----------|
| Between species and within temperatures: | |
| 100 <i>T. confusum</i> , 24° ÷ <i>T. castaneum</i> , 24° | 77.0% |
| 100 <i>T. confusum</i> , 29° ÷ <i>T. castaneum</i> , 29° | 76.6% |
| 100 <i>T. confusum</i> , 34° ÷ <i>T. castaneum</i> , 34° | 74.6% |
| Within species and between temperatures: | |
| 100 <i>T. confusum</i> , 24° ÷ <i>T. confusum</i> , 29° | 38.0% |
| 100 <i>T. confusum</i> , 24° ÷ <i>T. confusum</i> , 34° | 34.4% |
| 100 <i>T. confusum</i> , 29° ÷ <i>T. confusum</i> , 34° | 90.6% |
| 100 <i>T. castaneum</i> , 24° ÷ <i>T. castaneum</i> , 29° | 37.8% |
| 100 <i>T. castaneum</i> , 24° ÷ <i>T. castaneum</i> , 34° | 33.4% |
| 100 <i>T. castaneum</i> , 29° ÷ <i>T. castaneum</i> , 34° | 88.3% |

at 24° In terms of percentages (table IV), *T. castaneum* has approximately a

25 per cent higher fecundity rate although there is a suggestion that the egg production of *T. confusum* relative to *T. castaneum* increases slightly with decrease in temperature.

(2) As would be expected for median thermal ranges, the rate of oviposition becomes higher with increasing temperature. This is true for both beetles. At 24°, *T. confusum* exhibits a mean rate of 14.7 eggs per 72 hours; at 29°, 38.7 eggs, and at 34°, 42.7 eggs. Comparable means for *T. castaneum* are 19.1, 50.5, and 57.2. These differences in fecundity at different temperatures are all highly significant statistically (table III). The acceleration

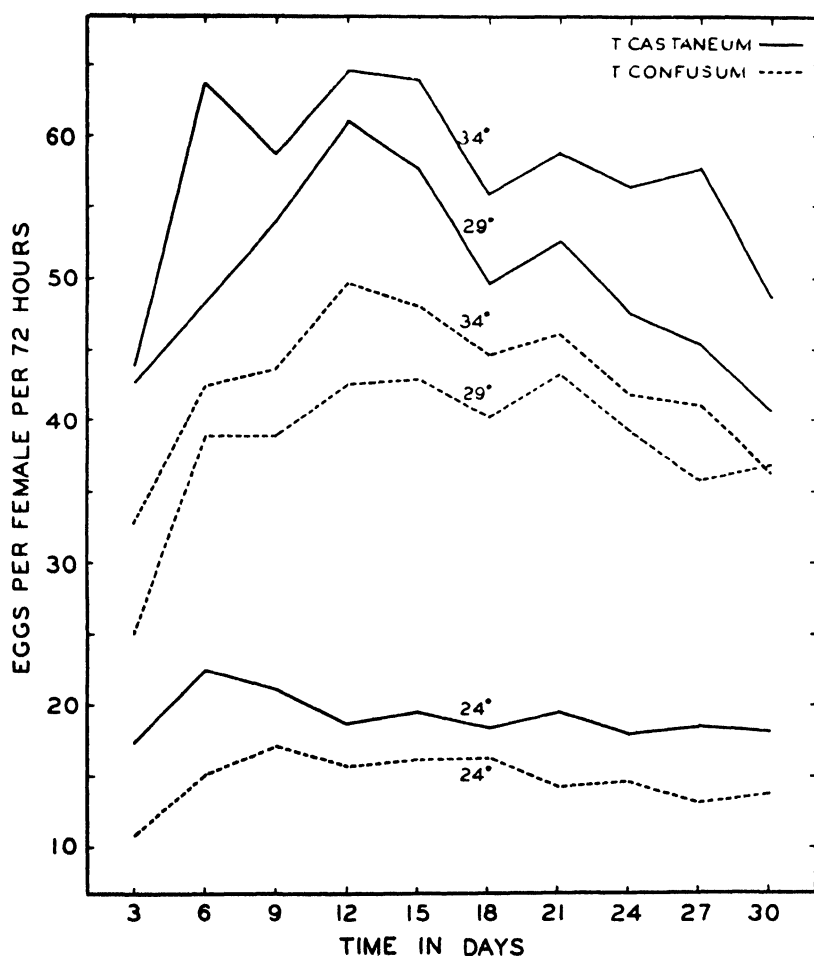


FIG. 1. Rate of oviposition graphed against time for *Tribolium confusum* and *T. castaneum* maintained at temperatures of 24°, 29°, and 34° C.

of oviposition is much greater when the temperature increases by 5° from 24° to 29° than when the increase is from 29° to 34° as seen in table IV. For example, at 24° the fecundity of *T. confusum* is only 38 per cent that of the fecundity at 29°, while the latter is 90 per cent of that obtaining at 34°. The same relations hold for *T. castaneum* with the possible exception that this species is slightly more favored at 34° relative to 29° than is *T. confusum*.

(3) Figure 1 depicts the pattern of oviposition by intervals. It is clear (a) that the first count is uniformly low; (b) that a peak in egg production characteristically occurs during the 6 to 15 day interval, and (c) that the decline in fecundity with time is more pronounced at the two higher temperatures than at 24°. In all curves, except that for *T. confusum* at 24°, there is a noticeable decline at 18 days with reference to the preceding 15 day count. This decline is of borderline significance for *T. castaneum* at 34° and 29° ($P = 0.0309$ and 0.0218 respectively) but is completely without

significance in the other instances ($P > 0.05$).

(4) There are no especially important patterns as regards variability. The standard deviations (table II) increase with temperature primarily because the means become larger, and, for the same reason, the standard deviations are somewhat higher for *T. castaneum* than for *T. confusum*. The coefficients of variability (table II) are largest at 24° for both species with negligible differences exhibited between the 29° and 34° samples.

RATE OF DEVELOPMENT

The data concerned with rate of development are presented in table V, that lists the duration of the egg, larval, and pupal stages of both *T. confusum* and *T. castaneum* at three temperatures; in table VI, that compares selected mean differences in these rates, and in table VII, that shows the percentage time spent in the various immature stages. Figure 2 graphs the essential information contained in table V.

Centering attention first on the dura-

TABLE V. *Biometric constants for rate of development of Tribolium confusum and Tribolium castaneum at temperatures of 24, 29, and 34° C.*

| Stage | Mean duration ± P.E. (hours) | S.D. (hrs.) | C.V. (%) | N | Mean duration ± P.E. (hours) | S.D. (hrs.) | C.V. (%) | N |
|-------------------------------------|------------------------------|-------------|----------|----|--------------------------------------|-------------|----------|----|
| <i>Tribolium confusum</i> at 24° C. | | | | | <i>Tribolium castaneum</i> at 24° C. | | | |
| Egg | 205.3±0.38 | 4.2 | 2.0 | 55 | 162.0 | | | 53 |
| Larval | 824.6±6.78 | 74.6 | 9.0 | 55 | 796.9±3.89 | 42.0 | 5.3 | 53 |
| Pupal | 260.0±7.00 | 7.7 | 3.0 | 55 | 249.2±0.97 | 10.5 | 4.2 | 53 |
| Total | 1289.9±7.19 | 79.1 | 6.1 | 55 | 1208.1±4.31 | 46.6 | 3.9 | 53 |
| <i>Tribolium confusum</i> at 29° C. | | | | | <i>Tribolium castaneum</i> at 29° C. | | | |
| Egg | 127.0 | | | 54 | 93.6±0.11 | 1.2 | 1.3 | 55 |
| Larval | 396.1±3.87 | 42.2 | 10.7 | 54 | 398.6±3.13 | 34.4 | 8.6 | 55 |
| Pupal | 138.9±1.54 | 16.8 | 12.1 | 54 | 121.7±1.89 | 20.8 | 17.1 | 55 |
| Total | 662.0±4.96 | 54.0 | 8.1 | 54 | 613.9±4.41 | 48.5 | 7.9 | 55 |
| <i>Tribolium confusum</i> at 34° C. | | | | | <i>Tribolium castaneum</i> at 34° C. | | | |
| Egg | 93.9±0.21 | 2.1 | 2.2 | 44 | 66.0±0.13 | 1.3 | 2.0 | 46 |
| Larval | 415.6±3.55 | 35.0 | 8.4 | 44 | 372.9±5.20 | 52.3 | 14.0 | 46 |
| Pupal | 118.4±0.99 | 9.8 | 8.3 | 44 | 99.4±0.81 | 8.1 | 8.2 | 46 |
| Total | 627.9±5.60 | 55.0 | 8.8 | 44 | 538.3±5.46 | 55.0 | 10.2 | 46 |

TABLE VI. *Selected statistical comparisons of the rates of development reported in table V*

| Comparison | Egg stage | | Larval stage | | Pupal stage | | Total period | |
|---|----------------------|-------|----------------------|-------|----------------------|-------|----------------------|-------|
| | Mean diff. ± P.E. | P. | Mean diff. ± P.E. | P. | Mean diff. ± P.E. | P. | Mean diff. ± P.E. | P. |
| <i>T. confusum</i> — <i>T. castaneum</i> , 24° | 43.3 | | 27.7 ± 7.8 | .0182 | 10.8 ± 1.2 | .0000 | 81.8 ± 8.4 | .0000 |
| <i>T. confusum</i> — <i>T. castaneum</i> , 29° | 33.4 | | *2.5 ± 5.0 | >.5 | 17.2 ± 2.4 | .0000 | 48.1 ± 6.6 | .0000 |
| <i>T. confusum</i> — <i>T. castaneum</i> , 34° | 27.9 ± 0.25 | .0000 | 42.8 ± 6.3 | .0000 | 19.0 ± 1.3 | .0000 | 89.7 ± 7.8 | .0000 |
| <i>T. confusum</i> , 24°–29° | 78.3 | | 428.5 ± 7.8 | .0000 | 121.1 ± 1.7 | .0000 | 627.9 ± 8.7 | .0000 |
| <i>T. confusum</i> , 29°–34° | 33.1 | | **19.5 ± 5.2 | .0126 | 20.5 ± 1.8 | .0000 | 34.1 ± 7.5 | .0024 |
| <i>T. castaneum</i> , 24°–29° | 68.4 | | 398.3 ± 5.0 | .0000 | 127.5 ± 2.1 | .0000 | 594.2 ± 6.2 | .0000 |
| <i>T. castaneum</i> , 29°–34° | 27.6 ± 0.17 | .0000 | 25.8 ± 6.1 | .0046 | 22.3 ± 2.1 | .0000 | 75.7 ± 7.0 | .0000 |

* The mean for *T. castaneum* higher.

** The mean for 34° higher than that for 29°.

tion of the total period of metamorphosis (the interval from laying of the egg to imaginal eclosion), it is evident that, at each of the three temperatures, *T. castaneum* passes through this development at a significantly faster rate than does *T. confusum*. It is equally evident from table V that development accelerates with increases in temperature. These two findings are similar to those already described for fecundity. There is also the suggestion that, in terms of rate of development,

T. confusum is slightly favored *relative* to *T. castaneum* at 24° while at 34° the reverse is true. In other words, an increase in temperature speeds up metamorphosis somewhat more for *T. castaneum* than would be expected on the hypothesis that both species have identical temperature optima. This physiological point may well be correlated with the geographical distribution of the two species discussed by Good ('36) who remarks: "Records in the United States indicate

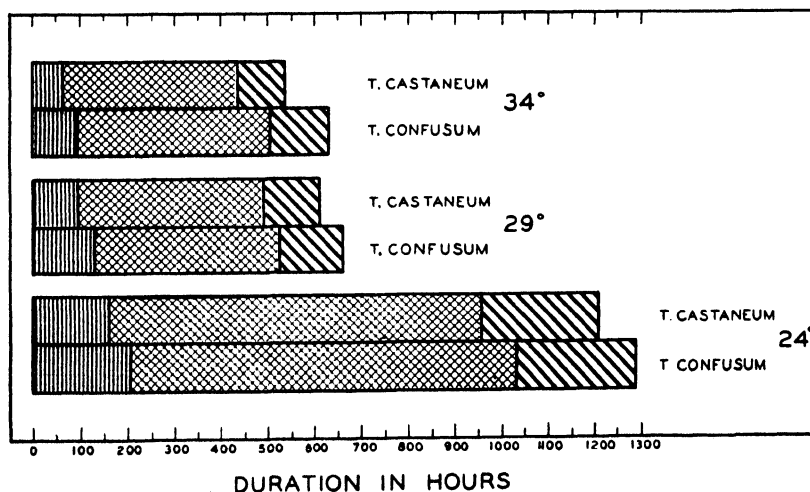


FIG. 2. Duration of the embryonic and post-embryonic stages of *Tribolium confusum* and *T. castaneum* at 24°, 29°, and 34° C. Left-hand boxes represent the egg stage; middle boxes the larval stage, and right-hand boxes the pupal stage.

that temperature has quite an effect on distribution. *T. castaneum* is essentially an insect of warm climates, and, although sometimes recorded from Canada and other northern countries, it is evidently not a permanent resident north of the fortieth parallel in eastern United States except in heated buildings. *T. confusum*, on the other hand, is more frequently found in the northern part of the United States than in the southern part. From 37° to about 40° N. both species occur commonly, while south of 37° *confusum* gradually become less common and in the Gulf States is largely replaced by *castaneum*."

At all three temperatures it takes longer for the egg and pupal stages of *T. confusum* to develop than it does for those of *T. castaneum*. The larval stages of the two species respond in similar fashion at 24° and 34°, namely: *T. confusum* larvae develop more slowly. At 29°, however, a deviation from this trend occurs—the two species requiring about the same number of hours to complete larval development. Thus, the greater total time spent in metamorphosis by *T. confusum* reflects at the lowest and highest temperatures significantly longer egg, larval, and pupal periods, while at 29° this greater time is to be accounted for by the egg and pupal stages only.

Table VII records the percentage time spent in the three stages. It can be stated in summary (a) that the larval stage consumes about two-thirds of the total developmental period; (b) that the egg stage is relatively longer for *T. confusum* at all temperatures and that the length of this stage relative to the total metamorphic period is greatest at 29°, and (c) that the pupal stage is essentially similar for both species as regards its percentage duration.

Several points worth noting can be made from scrutiny of the coefficients of variability listed in table V. Firstly, it is apparent that the relative variation descriptive of development is considerably less than that for fecundity (table II).

The latter coefficients characteristically have values in the 20 to 40 per cent range; the former are all below 20 per cent with modal values occurring below 10 per cent. A second point is that the egg stage is temporally less variable than the larval and pupal stages for both species. In fact, in two instances as indicated in table V, all eggs hatched within a single period of observation so that standard deviations and coefficients of variability could not be computed. Thirdly, there is some suggestion that variation is less at 24° than at 29° and 34°, the last two being quite similar in this respect. And finally, no important differences between species are evident.

SUMMARY

Data are presented on fecundity and rate of development of the flour beetles *Tribolium confusum* and *Tribolium castaneum* maintained at the three constant temperatures of 24°, 29°, and 34° C. It is shown for both species that fecundity increases and length of metamorphosis decreases as the temperature rises. It is further shown that *T. castaneum* has, as a species, a higher fecundity and a faster development than does *T. confusum* at all temperatures studied. There is a suggestion that the lowest temperature is relatively more favorable for *T. confusum*, and the highest temperature relatively more favorable for *T. castaneum*. The larval mortality of both beetles is increased by about 20 per cent when this stage is kept at 34°.

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NOTES AND COMMENT

HARDPAN DEVELOPMENT IN THE LANDES REGION OF FRANCE

The transformation between 1855 and 1875 of the Landes Region of southwest France from an unproductive, marshy, sandy plain of 2 million acres to a prosperous pinery still stands as the greatest reclamation and afforestation project in the world.

The maritime pine (*Pinus pinaster*) with which the Landes was planted has now been managed for more than a rotation as an even-aged, pure stand. Early and frequent thinnings reduce the stand to about 400 trees per acre at 20 years of age. At this age the trees are tapped for gum, and hardwoods and underbrush are weeded out of the turpentine stands. Periodic thinnings continue until there are approximately 120 trees per acre at the age of 70 to 80 years. The stands are then clear-cut and the cones scattered to obtain reproduction.

rial accumulated slowly because of excessive inundation during the winter and spring and extreme dryness in summer, and frequent fires during the dry season helped destroy the organic material that had accumulated. The infiltration capacity of the sandy soils was high and the water table was shallow, and consequently a hardpan layer started to develop. This was noticed prior to 1850, but was not considered important; its extent and depth before pine was planted are unknown. A reasonable estimate might be that 50 per cent of the region had some hardpan.

With a pure pine forest and better fire protection, the accumulation of the acid organic debris has increased, and so has the infiltration capacity. Rapid percolation of rainfall has carried large amounts of acid organic material down to the shallow water table. There it is

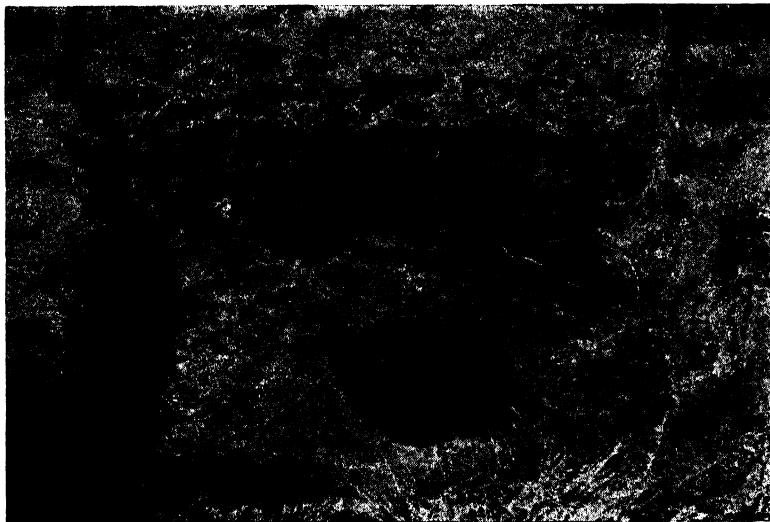


FIG. 1. Hardpan development in the Landes. The exposed mineral soil around the pit in the center is the beginning of the hardpan layer. The pit penetrates the layer to the coarse yellow sand below.

Today, this system of management does not appear satisfactory. The trees are less healthy and vigorous than before, growth is declining, gum yields have decreased, and natural reproduction is difficult, if not impossible, to obtain. An explanation of what may have caused this deterioration of the vegetation follows.

During the centuries before the Landes was drained, soil acidity increased. Organic mate-

deposited at depths of 25 to 90 centimeters. The hardpan layer (see fig. 1) now averages 30 to 40 centimeters in thickness and extends over 60 to 80 per cent of the Landes.

This layer hinders root development of the larger trees. The rather excessive accumulation of humus above the hardpan layer retards the establishment of natural pine reproduction. Internal soil drainage is also restricted. Dur-

ing wet periods of the year there are two water tables—one below and one above the hardpan layer.

In the summer of 1947, I examined typical Landes soil profiles with Professor Ph. Duchaufour of the École Nationale des Eaux et Forêts, Nancy, who will soon publish the results of his intensive investigations of the hardpan problem.

Professor Duchaufour's descriptions of typical soil profiles follow:

I. *Typical soil profile without hardpan development:*

- 0-4 cm. A₀ Black color
- 4-6 cm. A₁ Gray-black color pH 4.8
- 6-12 cm. A₂ Ash color pH 5.7
- 12-30 cm. A₃ Light yellow color
- 30-45 cm. B More compact without organic material, reddish brown color pH 5.8
- 45+ cm. C Coarse yellow sand

Ground cover species commonly found above this profile are *Pteris aquilina pubescens* and *Ulex europaeus*.

II. *Typical soil profile with hardpan development:*

- 0-15 cm. A₀ Very black color, many fibrous roots
- 15-25 cm. A₁ Light gray-black color with many roots pH 4.1
- A₂ Not differentiated
- 25-55 cm. B₁ Very black color. Organic accumulation. Beginning of hardpan layer pH 5.6
- 55-90 cm. B₂ Cemented layer of sand and organic deposits .. pH 5.7
- 90+ cm. C Coarse yellow sand and water table

Ground cover species commonly found above this profile are *Erica scoparia* and *Molinia caerulea*.

JOHN L. AREND

SOUTHERN FOREST EXPERIMENT STATION,
NEW ORLEANS, LOUISIANA

A SURVEY OF LITERATURE ON FUNGUS SOCIOLOGY AND ECOLOGY

INTRODUCTION

The literature of mycology is full of references to the habitat and season in which one can find higher fungi, especially the fungi found on the ground, but the literature of ecology has few papers on the ecology and sociology of the fungi. An article by Shantz and Piemeisel ('17) on the fungus fairy rings of eastern Colorado seems to be the first published work of ecological importance. Later Graham ('27) published one paper in which he discussed various aspects of the problems of fungus ecology in the Chicago region but did not use to any extent the quantitative methods of sociology. A year later a small book appeared in French by Gilbert ('28). Beyond a very few generalized papers in English on the problem, nothing further, to the writer's knowledge, appeared in the English language until 1937 when Wilkins and his associates initiated studies ('37, '38, '39, '40, '46) at Oxford University. Then Grainger ('46) published a few notes on the subject. The German literature suddenly assumed importance when Haas ('32) at Stuttgart, and Höfler ('37), Friedrich ('36, '37, '40) and Leischner-Siska ('39) in Vienna, published extensive studies based on quadrats established in Württemberg, near Salzburg, and near Vienna. A review of these German language papers follows.

The study of mycoecology has been nearly completely neglected in North America. Slipp and Snell ('44) treated the Boletaceae of the Kaniksu National Forest in relation to distri-

bution within different successional phases of the *Thuja-Tsuga* zone. The mycorrhizal relationships between this group of fungi and the trees with which they are presumably associated were emphasized. Baxter and Wadsworth ('39) and Baxter ('47) have studied extensively the ecological relationships of the fungi associated with the diseases of forest trees in Alaska by the use of line transects.

Nothing has yet been done in the way of intensive studies of fungi in the several vegetation zones, and in the several associations within these zones, from the quantitative sociologic point of view. Such studies would seem to be very interesting and important; constancy data collected during these studies would help to indicate mycorrhizal and other nutritional relationships, and therefore be applicable to various phases of forest ecology.

In the preparation of the following review the writer wishes to express his gratitude to R. F. Daubenmire who kindly criticized the manuscript, and to Mr. J. A. Stevenson, Mycological Collections, Bureau of Plant Industry, Soils, and Agricultural Engineering through whose co-operation photostats of the papers by Haas, Leischner-Siska and Friedrich were made available for study.

THE GERMAN LITERATURE

A large number of papers occur in the literature of phytopathology and mycology concerning the autecology of certain species and groups

of species of fungi. One of the most closely related of these to the synecology of the fleshy soil fungi is the paper by Shantz and Piemeisel ('17) on fairy rings, but this paper is concerned strictly with the fungi which form rings, their effect on the vegetation, and the formation of the rings; if other fungi also occur in the area of the ring, they are not considered of importance.

As far as this writer is aware, Haas ('32) published the first quantitative study of fungus populations to be found in the literature of ecology. Research in this field of ecology has been slow to get started partly because of the incomplete knowledge of systematics and partly because fungi commonly remain hidden within their substrata for long periods of time. Larger fungi of the soil fruit in only occasional years. Their mycelium may be present but not evident at other times; thus sociologic studies can be complete only when continued over a period of several years. The difficulty of identifying the sporophore after it is dry is a further discouragement since few people can work with such structures in this condition.

Haas has attempted to employ methods which were devised for sociologic studies of vascular plants using abundance and sociability of fruiting bodies as indices. To express abundance, the following six classes were devised: + only at one place in the forest plot, whether in a large cluster, fairy rings or singly, 1 at two places in the sample plot, 2 widely scattered, 3 irregularly dispersed, 4 rather generally scattered through the plot, and 5 in large masses common on the plot. Sociability classes included: 1 single specimens, 2 in small groups, 3 in large troops, 4 in rows, rings or some other special grouping, and 5 in numerous clusters or large groups.

Haas made 95 surveys of 46 plots in 1929, 1930 and 1931. In 1929 and 1930 only abundance records were kept but in 1931 both abundance and sociability data were obtained for many of the plots. Depending on the nature of the area he varied the size of his plots from 50×50 meters to 200×300 meters.

The presentation of the surveys made by Haas gives date of survey, location, the dominant and subordinate woody plants, the approximate age of the stand, the geologic substrate, the size of the plot, the exposure, and the vascular plants of the lower unions. This material, in tabular form, is followed by additional notes characterizing the area, and the fungi found on the plot are listed together with abundance and sociability class designations.

As a result of the surveys several types of fungus associations were discovered, these being correlated with the tree union and the geological substratum.

Of the conifer forests studied four principal tree species had been established in pure stands on one kind of sandstone. Each had a more or less characteristic fungus flora dominated by species definitely causing, or suspected of causing, mycorrhizae. *Gomphidius roscus* was believed to be more definitely associated with such *Boleti* as *Boletus flavidus* and *B. ovinus* than with the soil type or forest type.

In conifer forests on limestone the mycobiota is richer in species and number of individuals as compared to the sandstone areas. Certain species of the sandstone soils are absent and the number of individuals of the remaining species is increased. Still other species are restricted to limestone.

In deciduous forests the fungus flora was richer. This may be explained by the large number of fungi which appear to be associated with beech.

Naturally or artificially reforested quarries in Keuper sandstone areas where the fungi were more numerous and of somewhat different specific composition than the surrounding areas are taken to indicate areas where the influence of earlier deciduous forests was stronger.

In the Stuttgart area certain forests occur on marl, others on sandstone. While fungus species lists on each are long, those of sandstone are somewhat shorter than those of marl, but longer than lists of fungi on other sandstones because some limestone occurs banded in this sandstone. Fungus populations on moors and in forested areas characterized by heather and strong acidification correspond strikingly to the fungus populations on sandstone areas.

The surveys indicate that many species occurring on sandstone soils do not occur on limestone soils regardless of similarities in the floristic composition of the forests on these soils. When all surveys are tabulated it becomes evident that certain species are restricted to conifer forests and common to all types of conifer forests in the survey region; that certain species are restricted to sandstone and common to all sandstone plots surveyed; that some species are found only in spruce-fir forests, others only in scotch pine forests, and still others are restricted to those conifer forests growing on limestone soil.

Certain species are dependent upon the vegetation of an area through mycorrhizal relationship. From 48 to 72 per cent of the fungi on a plot could be expected to have mycorrhizal relationships. These species are particularly important in areas where the Ericaceae, Pyrolaceae and Orchidaceae are abundant. The fungi appear to be more characteristic in such locations since the herbaceous plants are reduced in quantity and number of species there.

A few fungi are associated with *Sphagnum* and other mosses. Several fungi grow on spe-

cial plant parts in the litter—*Marasmius fagctorum* on beech leaves, *Marasmius perforans* on spruce needles, and *Collybia esculenta* and *Pleurodon auriscalpium* (*Auriscalpium vulgare*) are dependent on buried or partially buried scotch pine cones.

As for the dependence on soil conditions it was noted that the greatest difference between lists of fungi on limestone and sandstone soils is found among the mycorrhizal species although the non-mycorrhizal species appear to have some preference for limestone or sandstone soils. (No studies of the pH of the soils in each plot were made.) A distinction can be made between species "peculiar to certain soils" and species "occurring on any soil." Another division appears between species which seem to prefer raw humus, such as can be found in conifer forests where the needles decompose slowly, and those which prefer mild humus such as that which is found in deciduous forests where the leaves decompose rather quickly. However, certain fungi, such as *Clitocybe laccata*, apparently can grow well in either type of soil. Some species are not found outside of the forest although others do occur outside where humus conditions are similar to those in the forest.

Zeuner ('22) had attempted earlier to differentiate between limestone and sandstone fungi. His classification does not carry over into the region studied by Haas who found some of Zeuner's limestone-loving fungi on sandstone.

The following classification summarizes Haas's findings in Württemberg. The species named in the key are ones that are representative of the habitat, and are not intended to include all the species found there.

I. Species associated with trees.

A. Through mycorrhizae.

1. With several tree species (conifer and deciduous forests).

a. On a wide variety of subsoil:

Boletus edulis, *Amanita rubescens*,
Russula alutacea.

b. Restricted to one type of subsoil:

Pholiota caperata, *Hydrocybe colus*,
Ramaria aurea.

2. With only one tree species (or at least in only the coniferous or deciduous forest).

a. On a wide variety of subsoil:

Lactarius blennius, *Russula queletii*,
Boletus elegans.

b. Restricted to one type of subsoil:

Russula puellaris, *Boletus tridentatus*,
B. satanas.

B. Indirectly through parasitic or symbiotic relationships with other soil fungi:

Gomphidius roseus, *Collybia tuberosa*,
Nyctalis parasitica.

C. Through special litter and duff requirements:

Mycena fagctorum, *Marasmius perforans*,
Pleurodon auriscalpium.

II. Species not associated with trees.

A. In close relationship with other forest plants (especially mosses):

Omphalia fibrula, *Galera hypnorum*, *Hygroclybe miniata*.

B. True saprophytes of the forest soil (humus plants).

1. On a wide variety of subsoil:

Clitocybe laccata, *Stropharia aeruginosa*,
Ramaria rugosa.

2. Restricted to one type of subsoil:

Clitocybe cyathiformis, *Inocybe corydalina*,
Thelophora terrestris.

For a number of years Karl Höfler ('37) was interested in developing research methods to study the phytosociology of fungi. The methods applied by Braun-Blanquet ('28) to the flowering plants must be modified for the fungi. Since the mycelium cannot be readily observed, only the fruit bodies can be studied. Also certain biological specializations of the fungi must be recognized: (1) parasitism, (2) saprophytism of the fungi on dead parts of vascular plants that remain in place, (3) saprophytism on litter (leaves, branches, needles), (4) loose union of the fungi in peritrophic mycorrhizae on the living tree, (5) strong nutritional symbiosis (mycorrhizae).

Fungus communities (unions) can be studied and named independently of other communities, and different fungus communities occur within the same forest association.

In carrying out his surveys Höfler used quadrats 10 × 10 m. In 1936 and 1937 the fungi were estimated quantitatively according to the Braun-Blanquet method combining estimates of abundance and constance. Thus all species received the symbol + or 1, amounting to the application of a mere two-part scale. This does not give the degree of dominance of the fungus vegetation. Since dominance data for autotrophic plants is of most significance as a measure of their success in obtaining light, whereas fungi are independent of light, dominance is of little value in mycoecology. Furthermore the superficial development of the fungus fruiting body remains small in comparison with the hidden development of the rest of the thallus so that this organ gives no hint of the relative importance of the species in the community.

In most genera a count of individual fruit bodies can be obtained without difficulty, but if one wants to obtain quantitative information on the relative importance of the species Höfler considers weighing indispensable. He collected all fruiting bodies of the fungi on a definite area quantitatively, sorted them into species, and weighed the fresh material of each species in the field.

Quadrats are characterized as to location, geological substratum, green vegetation associations, and history, height of forest, altitude, slope, forest floor, soil tests including pH and calcium carbonate content, etc. Fungi obtained on the quadrats at each visitation are listed in tabular form giving the name, number of individuals, fresh weight of all individuals, a special "abundance" symbol, and type of substratum.

In determining "abundance"¹ Höfler used a geometric mean derived by taking the square root of n (number of individuals) times g (weight of the number of individuals). "Abundance" class 4 signifies a value exceeding 200, 3 signifies the range 50-200, 2 signifies 7-50, 1 signifies less than 7. A fifth symbol + is used for one or two individuals of a small species or one individual of larger species on a quadrat.

Höfler had two students of whom Leischner-Siska ('39) published her complete report earlier than did Friedrich ('36, '37, '40). Leischner-Siska also pointed out the fact that the study of a single stand should be extended over an especially long interval. If several stands are compared they should be studied in the same year, preferably a "fungus year" in order to avoid "climatically caused vegetation fragments."

The fungus communities are dependent upon vascular plant populations so that surveys of both types are necessary. The type of fungus analysis used by Leischner-Siska included first the use of a combined scale for abundance and constancy, and second a sociability scale.

Sample plots were established in locations rich in fungi, and in other places representing special aspects of the phanerogamic vegetation. "It is shown further that the places which are richest in fungi are always poorest in phanerogams, and vice versa."

Arranged around Hellbrunn Hill near Salzburg were 13 research areas in which she located 23 permanent plots, each 10 × 10 m. The degree of vegetation cover, altitude, slope and pH are given.

A table comparing the number of species on the first seven plots on 9 of the visits shows the number of fungi inside and outside of the quadrats. This indicates that many more fungi occur on the whole stand than were included in the 100 sq. m. sample plot. Species numbers increase from early August to mid-September, then drop off; within that period there is an increase after each precipitation.

The data for all quadrats are tabulated on the basis of associations of higher plants. Of the 17 which lay in the *Fagetum praealpinum* 11 are strongly developed forest stands without shrub unions and with weak herb unions. In these 11 quadrats, which may be considered

parts of the same stand, 8 species of fungi have a high frequency value. In 91 per cent of the quadrats *Collybia radicata*, *Lactarius piperatus*, *Lycoperdon gemmatum* and *Mycena pura* occurred, and in 82 per cent of the quadrats *Clavaria pistillaris*, *Craterellus cornucopioides*, *Limacium eburneum* and *Russula fellea* occur. These eight species fall in a class value of V, basing frequency classes on units of 20 per cent. Of the remaining fungi found 11 species fell in frequency class IV, 25 in class III, 26 in II, and 70 in I.

Another result of this series of surveys was the discovery that *Pholiota caperata* in the area is associated almost exclusively with *Vaccinium myrtillus*. This hitherto unreported fact indicates a possible mycorrhizal relationship. In the *Abietum* and *Piceetum* this species was very scattered in the forest but dominant in the *Vaccinium* facies. This must still be considered as only a "parallel occurrence" since the mycorrhizal relationship has not yet been proved.

Friedrich's first paper ('36) on the ecology of the higher fungi lays special emphasis on the problem of scarcity of fungi in forests near Vienna in a dry season such as the fall of 1935.

Some fungi were found to be capable of fruiting in very dry periods. These are referred to as xerophilous species, although they also fruit in wetter periods, and include *Lactarius vellereus*, *L. piperatus*, *Hebeloma crustuliniforme*, *Boletus piperatus* and *Russula* spp.

Data were collected much in the manner of Höfler. An additional measurement was made on the amount of light available inside and outside the forest. One location at Rekawinkel in the Vienna Woods gave 60 Lux in a beech forest and 950 Lux under the open sky.

By measuring the soil moisture it was possible to delimit areas with similar water relations and these had similar fungus populations. A line delimiting an area of uniform soil moisture is referred to as an "isohygrophore." The few data presented indicate that at least certain fungi will fruit if the soil moisture is no more than 15-18 per cent but when moisture is reduced to 10-12 per cent no fruiting is observed.

During the coldest part of the winter when snow did not cover the ground it was found that while no fungi fruited in deciduous forests, certain species did fruit, and some in relatively large numbers, in evergreen conifer forests. This led to a study of the soil temperature. In one case on 27 November 1935 it was found that while near *Tricholoma nudum* the soil temperature amounted to 4.5° C., 180 cm. away it was only 3° C. Near *Clitocybe inversa* on 12 January 1936 the temperature of the soil was 3.4° C., 7 cm. away it was 3.3° C., and 80 cm. distant it was 2.9° C. The difference is attributed to the effect of the respiration of the soil mycelium.

¹ Dominance might have been a more appropriate term here.

In a mild wet spring following this fall season when many species did not fruit, there occurred a luxuriant out-of-season growth of many species. This was attributed to the large amount of food stored in the mycelium which created a readiness to fruit prematurely.

In a second paper on the ecology of the higher fungi Friedrich ('37) gives tables comparing 5-day temperature averages for September, October, and November in 1934, 1935, and 1936. He compares these averages with the 125-year average in order to emphasize the fact that the fall of 1936 was an unusually cold one. Five-day precipitation totals over the same periods indicate that the fall of 1936 was likewise an unusually wet autumn. However, fewer fungi than usual were obtained. In one area where the results of a 1934 foray produced 140 species in October, in 1936 only 16 species were obtained. It was shown that in limited areas in woods which were exposed directly to the sun, and in hollows protected from the wind, on the average more fungi were obtained than in places lacking these thermal advantages. Thus it was concluded that premature cold temperatures may prevent fruiting of all but those species which are cold resistant.

Later Friedrich ('40) elaborated further on the ecology of the higher fungi. It is again emphasized here that only the fruit body can be studied, that there may be a large amount of many species present which cannot be studied adequately. This is indicated by the great variety of fruit bodies which, according to the variation in the climatic conditions, appear in a variety of seasons over a period of years.

The studies reported in this last paper are of two types: autecologic and synecologic.

The study of habitat factors included water content of the substratum, effect of atmospheric precipitation, relative humidity, transpiration, indirect and direct action of the wind, temperature, light and soil.

Except for certain mycorrhizal and parasitic species, fungus mycelia rarely penetrate deeply into the soil. Fungi, then, are naturally dependent upon surface water. For those fungi whose mycelia remain in the highest soil layer constant irrigation is necessary. Rarely will fungi produce mycelia which penetrate to deep-lying moist layers of soil. In fungus-rich forests certain localities show complete absence of fungi. In forests which appear to be fungus free in general, small to large fungus oases appear. No excavation was done in Austria in relation to this problem but during army service in Poland it was observed during construction of trenches that water content in different parts of the forest may differ markedly. At one place in a two meter deep trench there was no trace of soil moisture, farther along the trench clearly wet ground extended to within several

cm. of the surface, and 50 m. farther the water stood 0.5 m. deep in the trench. Where the soil is bare the upper layers retain less moisture than where it is covered with vegetation which prevents rapid drying out by wind action and insolation. Some species of fungi grow in soil of low water content such as *Amanita muscaria* at moisture contents of 11 per cent,² *Lactarius vellereus* at 12 per cent, while others, such as *Craterellus cornucopioides*, do not grow in soil of less than 30 per cent water content. Near a waterfall where the soil is continually sprinkled with a fine spray minute fungi occur in thousands for several months. Litter and rotten wood hold water longer than the soil, and such habitats retain fungus populations longer.

Light rains are of little use to deeply rooted plants but are of great importance to the fungi whose mycelium near the surface absorbs the water rapidly. For this reason rainfall interception by the leaves of the canopy is very important to the soil fungi. Even dew is beneficial to fungi living in moss cushions. Prolonged rains are said to lead to the production of giant forms in a number of species.

For certain fungi at least, relative humidity is an important habitat factor. Fungi growing on damp soil reach complete development only in moist air. In the laboratory *Lepiota procera* stops development in a relative humidity of 35 per cent and below, but develops rapidly in relative humidities as high as 85 per cent.

Friedrich indicates that a number of workers have studied transpiration in fungus fruit bodies. Assumed protective adaptations of the fungi include the hairs of *Schizophyllum commune*, scales on caps of *Lepiota procera* and mucilagination of the cap surface of *Hygrophorus* species. Sporophores of most species of *Marasmius* are able to withstand prolonged desiccation without loss of function. Hydathode-like cystidia occur on the gills and caps of certain mushrooms. It has been supposed that transpiration from the underside of the cap is greater in contrast to the upper surface of the cap; however, this has been proved false experimentally.

Indirectly wind has serious effects on fungi through drying action on the soil. Between 22 November and 3 December 1937 strong winds reduced soil moisture from 47 to 29 per cent, litter moisture from 48 to 24 per cent, and stopped the emergence of sporophores.

Wind also has a direct action on fungi. When fungi project into the normal channel of the prevailing winds, as in the case of a dense cluster of *Hypholoma fasciculare* observed at the base of a tree trunk, they may be deformed by wind action although those which remained in the wind shadow were unharmed.

² These are no more than total water contents expressed on a fresh-weight basis.

Studies of the effect of wind on transpiration showed that larger specimens lose proportionately less of their water content than smaller, more delicate, specimens. A large fleshy species, *Hebeloma hiemale*, exposed to calm air at a relative humidity of 75 per cent at 7° C. lost 5.6 per cent of its weight after 1 hour; while in a wind of 1.5 m. per second under the same conditions it lost 26 per cent. The delicate species *Coprinus nycthemerus* protected from the wind, at a relative humidity of 60 per cent and a temperature of 19° C., lost 32-40 per cent of its weight, while at 3.3 m. per second under the same conditions it lost 305-320 per cent of its weight per hour through transpiration. In late October 1937 there appeared on walnut trees in a garden a number of specimens of *Pleurotus ostreatus*. Specimens on trees standing in the wind shadow of a house remained fresh while those on trees exposed to the west wind dried quickly.

Light seems related to the development of the fungus population. It was found that while certain species grew only where light was about 1/150 of full daylight, others were characteristic of forests with as much light as 1/4.

Certain species of fungi prefer sandy soil, others prefer loam. It was found that some species have a wide pH tolerance: *Amanita muscaria* pH 7.0-4.0; others have a narrow tolerance: *Mycena rosella* pH 4.5-4.3, *Lepiota procera* 6.6-6.0, *Tricholoma personatum* 7.5-7.2, *Stropharia aeruginosa* 8.5-8.0.

Friedrich's sociologic studies were based on permanent quadrats 10 × 10 m. These were laid out in forest areas which were described from the point of view of density of canopy, depth of litter and soil moisture. The green vegetation is listed according to unions, giving the abundance and sociability of the dominant members of each union. On each survey the date, relative humidity, air temperature, water content of the soil and fungi were recorded, and in some cases the soil character and temperature were observed. Comparative notes on the current precipitation and air temperature conditions at each survey were given where these were considered important. The fungi are listed with the number of individuals recorded.

Although some fungi may fruit out of season if the climatic conditions are unusual, the beech climax forest in the Vienna area exhibits a "*Russula* aspect" in mid-summer. Later in the summer a *Lactarius vellereus* aspect appears, and in late autumn at least seven species of *Mycena* comprise a "*Mycena* aspect." In other areas and at other times it can be said that a number of species are characteristic for short periods of time in a given season.

In September 1937 on a trip to Oetz in the Tyrol Friedrich collected the fungi in Oetz valley from the railroad station to the glacier region in the Venter and Gurgler Valleys. A list of species collected at each station on his route is given and the vegetation types are summarized briefly. Some of the results of this

TABLE I. A summary of some of the features of Friedrich's studies of altitudinal distribution (altitudes are in meters)

| Species | 600- 800 | 800- 1000 | 1000- 1200 | 1200- 1500 | 1500- 1700 | 1700- 1900 | 1900- 2200 | 2200- 2600* |
|---------------------------------|-------------|--------------|---------------|---------------|---------------|---------------|---------------|----------------|
| <i>Russula fragilis</i> | | | | | | | ----- | ----- |
| <i>Naucoria inquilina</i> | | | | | | | ----- | ----- |
| <i>Collybia asema</i> | | | | | | | ----- | ----- |
| <i>Hypholoma candolleianum</i> | | | | | | | ----- | ----- |
| <i>Hygrophorus pratensis</i> | | | | | | | ----- | ----- |
| <i>Lepiota amianthina</i> | | | | | | | ----- | ----- |
| <i>Nolanea pascua</i> | | | | | | | ----- | ----- |
| <i>Limacium lucorum</i> | | | | | | | ----- | ----- |
| <i>Boletus cavipes</i> | | ----- | | | | | ----- | ----- |
| <i>Lactarius aurantiacus</i> | | | | | | | ----- | ----- |
| <i>Dermocybe cinnamomea</i> | ----- | ----- | | | | | ----- | ----- |
| <i>Clitocybe laccata</i> | ----- | ----- | | | | | ----- | ----- |
| <i>Hygrophorus chlorophanus</i> | ----- | ----- | | | | | ----- | ----- |
| <i>Hebeloma crustuliniforme</i> | ----- | | | ----- | | | ----- | ----- |
| <i>Limacium chrysodon</i> | | | | | | | ----- | ----- |
| <i>Armillaria mellea</i> | | | | | | | ----- | ----- |
| <i>Limacium melizeum</i> | ----- | ----- | | | | | ----- | ----- |
| <i>Cantharellus cibarius</i> | ----- | ----- | | | | | ----- | ----- |
| <i>Mycena pura</i> | ----- | ----- | | | | | ----- | ----- |
| <i>Polyporus ovinus</i> | ----- | ----- | | | | | ----- | ----- |

----- present.

..... not found but probably present.

* Vascular plants of cushion form in this belt; forests dominated by conifers at lower altitudes.

study are shown in table I. With increasing altitude soil fungus density decreases. Above 1700 m. only scattered specimens occur, and these appear to be especially cold-resistant species. *Russula fragilis* (described by Singer as *R. septentrionalis* from north of the Arctic Circle) and *Naucoria inquilina* are the most important species near perpetual snow. Fungi occur as high as 3000 meters but only in places with favorable microclimate which are on south facing slopes. In a 50 sq. m. depression near a glacier at 2300 m., 55 individuals belonging to 12 species were found. Numerous specimens of 3 species were found in the wind shadow of a boulder. The soil temperature here was 11° C. whereas elsewhere it was 9° C. Many of the species are easily overlooked at high altitudes since they tend to become dwarf and their stipes are considerably shortened, making them difficult to tell from pebbles and stones among which they grow.

WM. BRIDGE COOKE

THE STATE COLLEGE OF WASHINGTON,
PULLMAN, WASHINGTON

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2,4-D EFFECTS IN CONNECTICUT VEGETATION, 1947

This paper is the second report on herbicide studies being carried out at Aton Forest, northwestern Connecticut. The first report (*Jour. For.*, 45: 449-452. 1947) presented the 1946 data on 27 woody species, resulting from appli-

cation of approximately 110 gallons of 0.15 per cent (1500 p.p.m.) solution of 2,4-dichlorophenoxy acetic acid. This second report presents the 1947 data on 63 species, after application of 400 gallons of 0.25 per cent (2500 p.p.m.)

solution of 2,4-dichlorophenoxy acetic acid. Preliminary data are included on other application techniques.

These herbicide studies are part of a larger long-term project in basic research on the establishment and maintenance of various semi-natural vegetation types. Lawn weeds are not considered. The bulk of the species studied are woody and rank weeds of fields, brushlands and forests. Techniques are being sought for widespread practical control of undesired plants.

Within the past year, numerous practical applications of the techniques here investigated have attained increased prominence. The following deserve mention: 1, wildlife management. Inasmuch as the maintaining of high populations of wildlife often depends on the preservation of certain marginal types of vegetation that are naturally unstable and temporary, herbicides offer a control of significant value. 2, control of rights-of-way of highways, railroads and utility lines. It now appears that many problems are not to be solved by a drastic though simple "kill-all" technique, which opens the site to soil erosion and to quick reinvasion by the unwanted species. Rather, the problem concerns the careful establishment of special dense low grasslands and thickets which can successfully keep out the undesired tall shrubs and trees. 3, control of fields, orchards and pastures. It is difficult to estimate the relationship of the abandonment of New England farm lands to the hitherto almost uncontrolled invasion by the forest. Modern herbicides are a tool which may well change many parts of the landscape. 4, forest management. Some of the most aggressive and undesirable weed trees are being found particularly susceptible to 2,4-D treatment.

METHODS

All applications were of 2,4-dichlorophenoxy-acetic acid (obtained as Garden Master Weed Killer, carrying 23 per cent acid). Two types of application were investigated: (1) droplet foliage-spraying; and (2) wood-painting.

1. Foliage-spraying. The commercial solution was diluted with water to 0.25 per cent (2500 p.p.m.). In special instances, stronger concentrations were used. Application was with a 3-gallon knapsack sprayer. Foliage was sprayed until completely wetted and drops began to roll from the leaves. First spraying of woody plants began May 21 (when the forest foliage was approximately half-expanded), and was continued actively through July 7 (decline of the peony and laurel flowers, and midst of the daisy season). Spraying was continued sporadically thereafter through August, but the foliage of woody plants had become hard and resistant, and herbaceous species had not only become resistant but the very quantity of foliage made greatly increased amounts of spray neces-

sary. Low shrubs (up to two feet) were sprayed in their entirety. Taller shrubs and trees had previously been cut during the winter, and the new shoots were sprayed. Spraying was done on all suitable days during the short season. Other than washing due to heavy rains shortly after the spraying, no significant permanent effects were observed from differences of humidity and temperature. All sprayings were in full or essentially full light. For experimental reasons, plants were generally not resprayed, so as to observe full effects of the single spraying.

2. Wood-painting. In July, August and the first week of September, a few preliminary tests were made in painting bared spots of wood at the bases of trees and of the major shoots of large shrubs. Equipped with a hatchet in the right hand and an oil can of 23 per cent 2,4-D in the left hand, by a few sharp strokes one removed the bark from two to four square inches (about one foot above the ground). A rough edge was left on the lower side to retain excess solution. A few squirts then wetted the entire cut surface. Only one such spot was made on each tree. With shrubs such as alder, only one or two of the shoots were treated with a single spot.

DATA

Indicative results were obtained with the following 63 species, arranged alphabetically by genus. The Latin nomenclature is that of Gray's Manual, 7th edition, and is followed by common names if such exist. Each species is designated as *v.r.* (very resistant), *r.* (resistant), *s.* (susceptible), or *v.s.* (very susceptible). Species are "very resistant" or "resistant" if killing is not effective with a single spraying, "susceptible" if kill is effective with a 0.25 per cent solution, and "very susceptible" if kill may be effected with a weaker solution. Killing is considered effective if 95 per cent of the shoots, or plants, appear killed at the end of the season. Special mention is made where wood-painting has been tried.

Acer rubrum, red maple (*v.r.*). Killing possible by several resprays, but impractical. Stronger sprays in early spring may be effective.

Acer saccharum, sugar maple (*r.*). Less resistant than red maple. Stronger sprays probably effective.

Alnus incana, speckled alder (*v.s.*). Sprouts from large shrubs that have been previously cut, are killed with a 0.15 per cent solution. Small shrubs killed by spraying. On August 15, about one dozen large shrubs were wood-painted, one shoot in each clump. By the end of the second week, the foliage of the painted shoot was entirely brown and crisped. At the end of the third week, adjacent shoots in the same clump had 0-95 per cent of the foliage brown.

At the end of the fourth week, it was noticed that the bark of the painted shoot and of one or more adjacent shoots had developed swollen yellowish spongy masses. Killing seems possible on refinement of technique for painting a single shoot of a large clump.

Apocynum androsaemifolium, spreading dogbane (s.). Partially susceptible in early spring. A 0.50 per cent solution in mid-June proved effective. A second spraying for new shoots from underground roots may be necessary.

Asclepias syriaca, common milkweed (r.). Spraying caused stem and leaf curvatures, followed by regrowth. A stronger solution would probably be effective.

Asplenium filix-femina, lady fern (r.). No effective kill. Stronger solutions in early spring may be successful.

Betula alba, paper birch (v.s.). Effective kill on seedlings. Wood-painting tests on 8-foot trees indicate susceptibility.

Betula lenta and *B. lutea*, black and yellow birches (v.s.). Effective kill on seedlings.

Betula populifolia, gray birch (v.s.). Effective kill on seedlings and on masses of shoots from stumps up to 8 inches in diameter. Wood-painting tests indicate susceptibility.

Cirsium arvense, Canada thistle (s.). Shoots effectively killed when small. Resprays necessary as new shoots arise from underground parts.

Cirsium lanceolatum, bull thistle (s.). Kill is practical in early spring, before height growth occurs.

Cornus alternifolia, alternate-leaved dogwood (s.). Several 3-foot plants apparently killed.

Crataegus macrosperma type, hawthorn (s.). Several 3-foot seedlings apparently killed.

Dicksonia punctilobula, hay-scented fern (r.). No effective kill. Stronger solutions in early spring may be successful.

Digitaria sanguinalis, crabgrass (v.r.). A 0.25 per cent spray not effective. A 23 per cent solution squirted on basal third of culms resulted in death, as evidenced by tests on some two dozen plants on bare trail-edge. Tests on several other grasses give preliminary indications that 23 per cent solution will kill tissue where contact is made, but that the solution is not conducted sufficiently to other parts of the plant for effective kill.

Fraxinus americana, white ash (v.r.). Sprays of 0.25, 0.50, and 1.00 per cent only caused cessation of leaf growth and curvature, followed by apparently normal growth. On July 24, several 2-foot seedlings were sprayed with an 11.5 per cent solution, which burned the foliage brown in about one week, and by late fall had killed at least all the above ground parts. In early August, about a dozen young trees were decapitated, and the cut ends painted with 23 per cent 2,4-D. By early September

these cut plants had resprouted, and death during the following winter is problematic.

Gaylussacia baccata, huckleberry (r.). Part of the resistance may be due to the fact that this species is one of the last to leaf out in spring, and may be missed in early spraying. Stronger solution is recommended when leaves of this species are half expanded.

Hemerocallis fulva, day lily (v.r.). Stronger spray may be effective if repeated.

Hypericum perforatum, St. Johnswort (s.). Possibly a 0.15 per cent solution would be sufficient. An aggressive and potentially predominant weed.

Ilex verticillata, winterberry (r.). Killing spotty and unsatisfactory. Stronger solutions recommended.

Juniperus communis var. *depressa*, low juniper (v.r.). No effective kill, though foliage yellowed. Stronger solutions may be effective.

Juniperus virginiana, red-cedar (r.). One three-foot plant sprayed. No effective kill, though entire foliage died, followed by regrowth. Stronger solutions may be effective.

Kalmia angustifolia, sheep laurel (s.). Apparently effective kill by end of season, at least of above ground parts.

Kalmia latifolia, mountain laurel (v.r.). Solutions up to 0.5 per cent caused only withering, curvature, and cessation of growth of the younger foliage. Wood-painting on larger shrubs should be tried.

Lycopodium complanatum var. *flabelliforme*, ground-cedar (r.). Stronger solutions may be effective.

Lyonia ligustrina, male berry (v.r.). Plants sprayed early in spring recovered fully. Much stronger spray may be effective.

Oakesia sessilifolia (s.). Susceptible in early spring. Stronger spray recommended for general killing.

Onoclea sensibilis, sensitive fern (s.). Effective kill in early spring only. Thereafter, stronger solutions may be effective.

Osmunda claytoniana, interrupted fern (s.). Susceptible only in early spring. Resistant when fronds are fully expanded. Stronger spray recommended.

Picea abies, Norway spruce (s.). Seedlings susceptible when foliage completely wetted.

Pinus strobus, white pine (s.). Susceptible when foliage completely wetted, for seedlings up to three feet in height.

Populus grandidentata, large-toothed aspen (s.). Effective kill on several three-foot seedlings in early spring.

Populus tremuloides, trembling aspen (r.). Effective kill in very early spring. Not effective when foliage has first matured. Summer wood-painting tests on trees 30 feet high showed no results by autumn.

Potentilla canadensis, cinquefoil (v.s.). Always complete kill in clumps of sprayed Spiraea.

Potentilla fruticosa, shrubby cinquefoil (s.). Apparently effective kill, though reactions are slow.

Prunus pennsylvanica, fire cherry (v.s.). Roots from large stumps send up suckers which must be resprayed. Preliminary wood-painting tests on a 12-foot tree, August 1, apparently successful in that all foliage was brown and crisped two weeks later. A test on a 30-foot tree, September 8, caused premature coloration of entire tree one week later, and possibly death.

Prunus serotina, black cherry (s.). Seedlings apparently killed.

Prunus virginiana, choke cherry (s.). Shoots satisfactorily killed if sprayed in early spring. Otherwise partially resistant. Preliminary tests on wood-painting, in August, of 8-foot shoots, caused foliage to dry and remain persistent after normal leaf-fall of control plants.

Pteris aquilina, bracken (v.r.). Some kill in earliest spring sprayings. Later sprayings resulted in stem curvatures, followed by recovery. Stronger solutions in early spring may be successful. A 0.5 per cent spray later in the season had no effect.

Pyrus communis, pear (r.). Foliage entirely dried, but wood not killed. Stronger spray recommended.

Pyrus malus, apple (v.r.). Reactions variable. Stronger sprays recommended.

Quercus rubra, northern red oak (r.). Stronger solutions may be effective. A wood-painting test, August first, on a six-inch-diameter 30-foot tree showed sensitivity, and remarkable specificity in the flow of the acid directly above the point of application. In two weeks, a large branch 10 feet directly above the wound had half-browned. Five weeks later, the branch was entirely brown, and other parts of the tree were browning prematurely. Recovery expected.

Rhus typhina, staghorn sumach (v.s.). New shoots from underground roots make second or third sprayings necessary. Six-foot high plants killed with a 0.15 per cent solution. A three-foot shoot from an old rootstock sprayed August 27 with a 1.0 per cent solution apparently killed, indicating that late-season spraying is possible for this species.

Rubus allegheniensis, blackberry (v.r.). A 0.25 per cent solution wilts foliage, causes curvature, followed by regrowth. Stronger solutions were used later on the same plants. A 1.00 per cent solution, applied August 27, also appeared ineffective. Recovery sometimes by appearance of new primocanes. Stronger solutions in early spring may be effective. An 11.5 per cent solution, accidentally applied to several plants on July 24, appears effective.

Rubus idaeus var. *aculeatissimus*, red raspberry (v.r.). Foliage appears less resistant

than that of blackberry. Stronger solutions must be used for effective kill.

Rubus odoratus, flowering raspberry (s.). One plant treated, and killed. A 0.15 per cent spray is insufficient.

Salix cordata (v.s.). Apparently complete kill. Preliminary tests indicate that perhaps spraying of only half the plant (as from standing in one position only) would be sufficient.

Salix discolor, pussy willow (v.s.). Same as for *S. cordata*. Shoots from rootstocks that had borne 12-foot shrubs were apparently killed.

Salix rostrata (v.s.). Same as for *S. cordata*.

Sambucus canadensis, common elder (s.). Seedlings and young plants probably susceptible. Suckers from large root system apparently killed only after second spraying.

Sedum purpureum, live-forever (r.). Shoots dying, but plant recovering. Stronger spray may be effective.

Solanum dulcamara, nightshade (r.). Growth continued with little interruption. Stronger spray recommended.

Solidago graminifolia, goldenrod (s.). Plants easily killed in early spring. Foliage in mid-summer resistant.

Solidago rugosa, goldenrod (s.). Plants easily killed in early spring. Rank foliage of mid-summer not only resistant, but requiring large quantities of spray.

Spiraea latifolia, meadowsweet (s.-v.s.). In early spring a 0.15 per cent is sufficient. An abundant weed, easily controlled.

Spiraea tomentosa, hardhack (s.). Tall plants should be cut before the growing season, and the small shoots sprayed in early spring.

Tilia americana, basswood (s.). Susceptible, as evidenced from two sprayed three-foot seedlings.

Ulmus americana, American elm (s.). Several seedlings effectively killed.

Vaccinium corymbosum, high blueberry (s.). Apparently complete kill on shoots from plants cut during the preceding winter. Early spring spraying with weaker solution sometimes also effective.

Vaccinium pennsylvanicum, low blueberry (s.). Apparently complete kill. Early spring spraying with weaker solution sometimes also effective.

Verbascum thapsus, mullein (s.). Spraying of basal rosettes of first-year plants resulted in complete kill.

Viburnum lentago, nannyberry (s.). Suckers near base of large shrub cut in preceding winter; shoots sprayed in spring. Apparently effective kill of the sucker plants.

CONCLUSIONS AND RECOMMENDATIONS

Present studies indicate that 2,4-D is a suitable herbicide for controlling most of the woody

and rank weeds of fields and orchards. Forty-one species are classed as "susceptible" and "very susceptible," 22 species as "resistant" and "very resistant" to spraying with a solution of 0.25 per cent. For overall spraying of undesired species, a solution of 0.5 per cent is recommended.

Brush-cutting preliminary to spraying is recommended for all shrubs over two feet in height, and for all larger plants which send up shoots suitable for spraying. Such preliminary cutting not only markedly reduces the amount of spray necessary, but reduces the possibility of spray-drift damaging other plants. Furthermore, it reduces the possibility of spray not reaching all parts of the foliage and of the plants below, a situation lessening the effective kill. Large trees of certain species may be left for wood-painting treatment, if known to be susceptible.

The preferred spraying season for this region is from mid-May through June, i.e. from the time the foliage is half expanded to the time when the daisies, peonies, and laurel are in full bloom, when the first day lily appears, and the hawkweeds have passed. For species very susceptible to 2,4-D (such as willows, alders, birches, and sumach), spraying can be light, and perhaps restricted to one side of the plant. After June, the rank weeds have produced so much growth that far more spray is needed,

and the foliage is more resistant. For woody plants, foliage in July is generally hard and resistant.

Selective post-season spraying is possible when the individual characteristics of the species are known and make it practicable. For example, willows, alders, birches and sumach can probably be treated, through July at least, with a stronger solution.

From preliminary tests, it appears that wood-painting may be feasible in July and August, at times when other treatments are not effective. One should also investigate the effects of wood-painting in April and early May, before the leaves have expanded. Species which presumably will react to this simple technique are fire cherry, choke cherry, alder, paper birch, gray birch, sumach, and pussy willow.

Care must be exercised in anticipating the increased growth of resistant species when competition of non-resistant species is removed. For example, mixtures of blackberry, ash, willow and alder, if sprayed, may result in dense stands of blackberry or young ash, or both, a type possibly as unwanted as the original community.

Further tests are being planned for 1948, using varied combinations of applications, chemicals, light conditions, and seasons.

FRANK E. EGLER

ATON FOREST,
NORFOLK, CONNECTICUT

THE VERTICAL DISTRIBUTION OF PHYTOPLANKTON AND THE THERMOCLINE

By taking water samples from different depths in a lake and investigating the phytoplankton, either by estimating the number of algal cells or by measuring the chlorophyll content, we obtain a diagram of distribution which is the result of several different factors. Many other biological processes in the lake depend in turn on the vertical stratification of phytoplankton. We may begin to understand these stratifications if we imagine them to give, not a stationary picture, but a dynamic one, somewhat like a stream. In the upper water layers, where the light is of sufficient intensity for photosynthesis, a continuous multiplication of cells takes place and causes the *flow* of phytoplankton organisms; at depth, on the other hand, there results a *runoff* of dying and sinking cells. Therefore, the form of the vertical distribution is determined in the main by (1) the rate of multiplication of cells and (2) their sinking speed. Rapid multiplication with low sinking speed causes accumulation of cells in the upper water. Slow multiplication combined with rapid sinking, conversely, results in uniform vertical distribution. As both factors are modified in many ways by environmental influences, an al-

most infinite variety of distribution patterns is to be expected, and is actually observed. None the less, certain regularities may be recognized.

Of all the factors which influence the sinking speed of plankton, turbulence plays the chief rôle, for with the exception of those like the Cyanophyceae, which are lighter than water, cells will sink more rapidly in quiet than in turbulent or running water. As is well known, ordinary lakes are divided by the thermocline into two layers. The water masses above the thermocline—the epilimnion—are always turbulent under the influence of the wind and their own diurnal thermal circulation, while those below the thermocline—the hypolimnion—are relatively calm. (This calm is only relative, however, for even here a certain amount of turbulence is caused by internal waves.)

Investigations and calculations undertaken in Lake Constance (Bodensee) show, as expected, that the sinking velocity of planktonic diatoms is much lower in the epilimnion than in the hypolimnion (table I):

It appears, then, that phytoplankton cells sink on the average about ten times faster in the hypolimnion than in the epilimnion. For this

TABLE I. *Sinking speed (in m. per day) of diatoms in different depths of Lake Constance (after Grim)*

| Depth, m. | <i>Synedra acus</i> f. <i>delicatissima</i> | <i>Cyclotella</i> sp. (dead) |
|-----------|---|------------------------------|
| 10-15 | 0.5 | 2.5 |
| 15-20 | 1-1.5 | 3.0 |
| 25-30 | 4-5 | 3.5 |
| 30-50 | — | 5.0 |
| 50-100 | — | 7.0 |
| 100-200 | 20 | 8.0 |

reason we consider that the position of the thermocline is of fundamental importance for plankton distribution. If the thermocline lies so deep that the bulk of the reproduction of phytoplankters takes place in the epilimnion, then the layer of maximal cell concentration will remain there for a long time. But if the thermocline is near the surface, so that plankton multiplication occurs in greater depths, the layers of maximal plankton content will be rapidly depleted of plankton by sinking. The latter relationship will be intensified if the water is very transparent, for the phytoplankton consists chiefly of shade-algae, which are injured by the high light intensity at the surface.

These considerations are clearly borne out by a comparison of two lakes in Bavaria, namely Würm Lake (Würmsees or Starnbergersee) and Königs Lake (Königsee). The first is situated in the Alpine foreland south of Munich, while the second lies in a deep, narrow valley and is therefore protected from wind (fig. 1). Hydrographic data for the two lakes are given in table II.

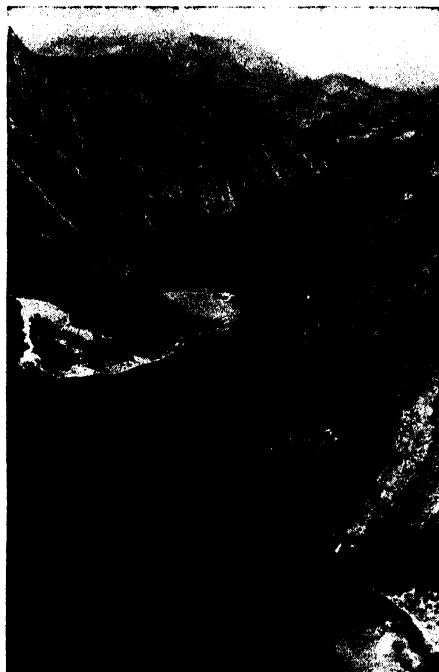


FIG. 1. Königs Lake in Bavaria, seen from its southern end.

The vertical distribution of plankton has been established for 1942 and 1947 by means of chlorophyll determinations (for methods, see Man-

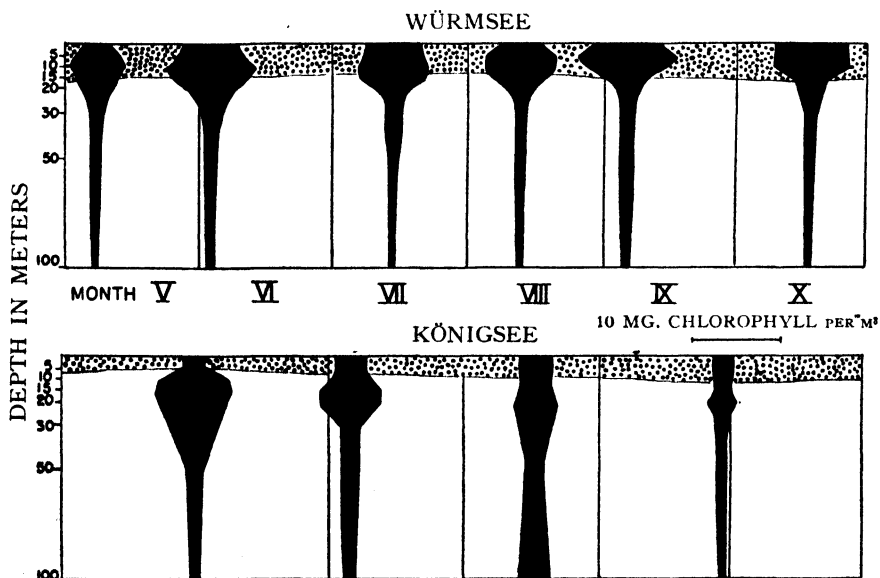


FIG. 2. Vertical distribution of phytoplankton (chlorophyll content) in Würmsees and Königsee. The stippled area represents the homothermal surface layer (epilimnion).

TABLE II. *Hydrographic data*

| | Würmsee | Königsee |
|-------------------------------|---------|----------|
| Area, km. ² | 57.0 | 5.2 |
| Maximum depth, m. | 123.0 | 188.2 |
| Mean depth, m. | 54.0 | 93.1 |
| Depth of thermocline | 15-20 | 3-8 |
| Transparency, m. | 3.5-4 | 11-12 |
| Elevation above sea level, m. | 584 | 602 |

ning and Juday, '41, and Gessner, '44). The great difference between the two lakes is clearly apparent in figure 2. Würmsee shows the distribution scheme characteristic of all the larger lakes in the Alpine foreland of Bavaria (Lake Constance, Ammersee, Chiemsee), i.e., (1) a maximum of plankton in the epilimnion with a rapid fall in the thermocline, and (2) a very constant vertical distribution throughout the summer. The epilimnial phytoplankton maximum disappears only when the thermocline disappears, in late autumn or winter.

Conditions in Königsee are quite different. Here the thermocline lies very high (fig. 3), because of the sheltered situation, and because the transparency is also great we find the plankton maximum in the thermocline or just below. Comparison of the diagrams for plankton in the whole water column (fig. 2) shows that in spring the standing crop in Königsee is by no means poorer than in Würmsee, and the species are the same in both lakes (*Synedra acus* forma *delicatissima*, *Asterionella formosa*, *Cyclotella* sp.). With the advancing season two features become evident in Königsee: (1) shrinkage of the maximum, and (2) its down-

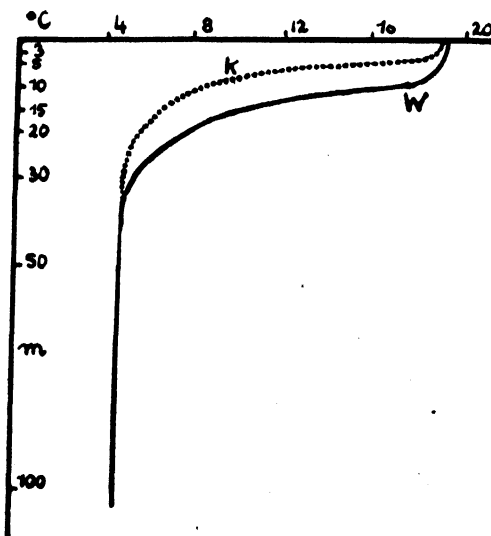


FIG. 3. Temperature curves for Königsee (K) and Würmsee (W) during the summer months.

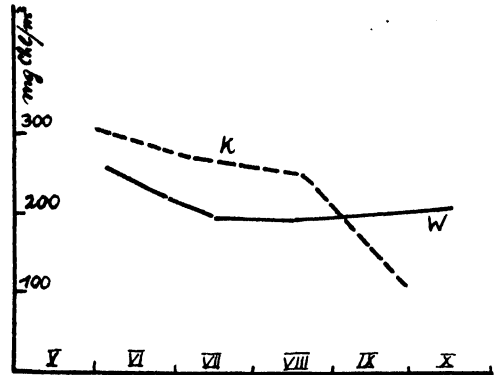


FIG. 4. Chlorophyll content of a water column 100 m. long under 1 m.² in Würmsee (W) and Königsee (K) during the summer.

ward displacement. In May the plankton maximum of 8.4 mg. of chlorophyll per m.³ lies at about 15 m.; by the end of September it has decreased to 3 mg. per m.³ and has sunk to 20 m.

In figure 4 the total quantity of chlorophyll in a water column 100 m. long under 1 m.² of lake surface is shown for the two lakes. There is a small decrease in both lakes at first. But while the values for Würmsee remain essentially constant, there is a sharp decrease in Königsee in September. This comes about because the late summer plankton, descended from the early spring maximum, has sunk below the 100-m. limit and is not included in the curve.

The difference between the two lakes becomes even more distinct when the mean depth of the phytoplankton is plotted according to the advancing season. By "mean depth" we mean the depth above and below which are found half the total quantity of plankton in the stand-

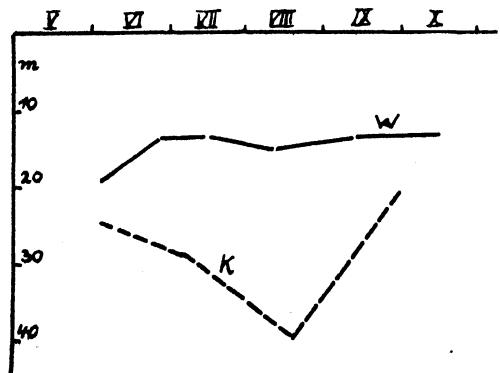


FIG. 5. Mean depth of phytoplankton in Würmsee (W) and Königsee (K) during the summer.

ard 100 m.² water column. This mean depth is approximately constant in Würmsees during the whole summer, while in Königsee it falls steeply as a result of the higher sinking speed. The mean depth rises again in autumn because the spring maximum has sunk below 100 m. and the mean depth is controlled by the relatively small increment nearer the surface.

The summer of 1947 was especially favorable for such observations, being exceptionally free from rainfall. The stratification of plankton can be significantly changed by rainfall in a very short time, for on the one hand the mass of plankton can be increased by the importation of nutrient salts, while on the other hand plankton can be spilled out of the lake. The smaller the lake, the more strongly these effects should be expressed. We would therefore expect very different standing crops in successive years in Königsee, and table III shows that this is the case:

TABLE III. *Chlorophyll content in Königsee (mg./m.³)*

| Depth, m. | 0 | 5 | 10 | 15 | 20 | 30 | 50 |
|-------------------|-----|-----|-----|-----|-----|-----|-----|
| September 2, 1941 | 3.5 | 4.3 | 5.4 | 8.0 | — | 3.2 | 4.0 |
| July 30, 1942 | 0.4 | 0.2 | 0.7 | — | 1.0 | 0.5 | — |

The high values in September 1941 were surely caused by the extremely high rainfall in August 1941, and the extraordinarily low values in July 1942 indicate that even so early in the season it can sometimes happen that the spring maximum has sunk to the bottom.

This comparison of the vertical distribution of phytoplankton in two lakes shows clearly how the biological character of a lake depends not only on its chemistry but also on the geography of its environment.

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Fritz GESSNER

WOLTERECK BIOLOGICAL LABORATORY,
SEER, BAVARIA

RELATIONSHIP BETWEEN FREQUENCY INDEX AND POPULATION DENSITY

Frequency index, which is the proportion of samples in which a given species appears, is related to population density, as is well known. The more dense the population the greater the proportion of samples in which the species will appear. The relationship between population density and frequency index, however, is not directly proportional, as has been pointed out by several ecologists (Kylin, '26; Blackman, '35; Ashby, '35). A mathematical treatment of the relationship has been presented by Fisher ('41, sec. 17).

In his original proposal of frequency index, Raunkiaer ('09) suggested that this index would be widely useful for the study of vegetational changes. Later it was learned that the relationship between frequency and population density is regular only when the distribution of the species concerned is at random. From a study of European grasslands and other communities Blackman ('35) concluded that many, but not all, species of plants are distributed at random and consequently that the density often can be computed from the absence index (1.0 minus the frequency index).

It has been asserted by Cole ('46), however, that populations of organisms living in nature

are only rarely distributed at random. My own observations support this statement and suggest that the distribution of most kinds of animals and plants is non-random, except over small areas in very uniform habitats.

It is desirable then to determine how much error can result from the calculation of population density from frequency counts made of populations which are not distributed at random. In table I are presented counts of the number of individuals of three species of plants on four blocks within each of which 25 sample plots were taken at random. The percentage of sampling was therefore 5.0. The plants counted were (1) the fruiting stocks of wild carrot (*Daucus carota*); (2) the dead fruiting stocks of yarrow (*Achillea*), but not the young plants which lacked fruiting stocks; and (3) both young and old plants of the ironweed (*Vernonia*). The observations were made on September 10, 1947, on a gently sloping grass and herb-covered field on the Edwin S. George Reserve, near Pinckney, in southern Michigan. The area sampled was 100 yards long by 20 yards wide, marked down the longitudinal axis by a surveyor's tape. This area was divided equally into four blocks, each 50 × 10 yards in

TABLE I. *Relation of density to frequency index in three species of plants*

Counts made on square-yard plots taken at random in four adjacent blocks in an open field on the Edwin S. George Reserve, September 10, 1947

| Species | Block | Number of samples | Frequency index | Mean per sample calculated from frequency index | Actual mean per sample plot | Variance | Chi-square of deviation from Poisson series (d.f. = 5) |
|-------------|-------|-------------------|-----------------|---|-----------------------------|----------|--|
| Wild carrot | A | 25 | .44 | .58 | 1.88 | 11.32 | — |
| | B | 25 | .44 | .58 | 0.72 | 1.04 | — |
| | C | 25 | .40 | .51 | 0.72 | 1.13 | — |
| | D | 25 | .32 | .39 | 1.20 | 10.83 | — |
| | Total | 100 | .40 | .51 | 1.07 | 6.05 | 89.55 |
| Ironweed | A | 25 | .24 | .27 | 0.68 | 3.56 | — |
| | B | 25 | .04 | .04 | 0.48 | 5.80 | — |
| | C | 25 | .56 | .82 | 1.52 | 5.75 | — |
| | D | 25 | .32 | .39 | 0.76 | 1.52 | — |
| | Total | 100 | .29 | .34 | 0.86 | 3.92 | 838.05 |
| Yarrow | A | 25 | .44 | .58 | 1.52 | 6.01 | — |
| | B | 25 | .40 | .51 | 1.32 | 3.56 | — |
| | C | 25 | .32 | .39 | 1.32 | 3.67 | — |
| | D | 25 | .12 | .13 | 0.24 | 0.48 | — |
| | Total | 100 | .32 | .39 | 1.10 | 4.05 | 270.99 |

size. Each sample plot was one square yard in size and was outlined by a light wooden frame. Each sample plot was located by pacing from the appropriate point along the axial tape to the corner position of the plot. The position of each sample plot was determined by the drawing of numbered cards. John A. King and Elizabeth J. Dice assisted with the counting.

From table I it is evident that neither of these three species of plant under consideration is distributed at random over the area sampled. In a random distribution (Poisson series) the variances should be the same as the means. The actual variances of the counts on the sample plots, however, exceed the means on every block and for every species, showing that the plants tend to occur in groups (contagious distribution). Inspection of the field in which the counts were made indicated that each of the three species of plants was more abundant in some parts of the field than in others, presumably due in part to local variations in the character of the soil and in the slope exposure.

It is not practical to calculate directly the statistical significance of the differences between the variances and the means of the sample counts. The significance of the deviation from a Poisson series may, however, be calculated by chi-square (Snedecor, '46: 441). Because of the small numbers in some items, the chi-squares have not been calculated for each block. For the total sample counts of each species, however, the chi-squares indicate that the deviation from random of the distribution of each of the three species of plants is highly significant.

Because of the non-random distribution of the individual plants over the plots examined the calculations of their mean population densities from their frequencies give figures that are inaccurate. In every block the estimates of population density, calculated from the number of samples lacking any representative of the form, is much lower for each of the three species than the more accurate estimates made by counting all the individuals on the same sample plots. This result is due to the tendency of these plants toward clumping, with a consequent excess of samples in which no example of the given species occurs. In none of the blocks examined does the mean calculated from the frequency amount to much more than about two-thirds of the counted mean. For most of the blocks and species the calculated means are only about half the values obtained from the actual counts. At the greatest extreme, the calculated density of ironweed in block B is only about one-tenth the density shown by the complete counts per plot. Such extreme errors of estimate as these could seldom be tolerated in field work.

It is evident, therefore, that the calculation of the population density of a species from the frequency of its occurrence in samples of any kind may give very erroneous figures when the distribution of the form is non-random. Unless the distribution of the species concerned is known to be approximately at random over the area studied, therefore, frequency should not be used as an indication of population density.

SUMMARY

From counts made of three species of plants on a series of random, yard-square plots in a field in southern Michigan, it is shown that neither of the three species is distributed at random over the area. The frequency index of each species, consequently, gives a very erroneous estimate of its population density. The densities calculated from the frequency indexes range from about two-thirds to less than one-tenth of the actual densities obtained by counts of the individuals.

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LEE R. DICE

LABORATORY OF VERTEBRATE BIOLOGY,
UNIVERSITY OF MICHIGAN

WATER-LIKE SURFACES ATTRACT VOLANT DESERT ANIMALS

The entrapment of animals on freshly oiled roads and oil pools has frequently been recorded in the literature. Koestner ('42) found fifteen bats and several birds trapped by a freshly oiled road. The road was shaded from both sides by trees and the bats probably mistook the oil for water. Miller ('30) tells of the entrapment of dragon flies in the La Brea Tar Pits. The insects became stuck while attempting oviposition. Koestner (*loc. cit.*) and Hubbs ('47) have stated that where road oiling is practiced it may prove to be an effective means of obtaining museum specimens. These writers also pointed out the possibility of using oiling as an aid in obtaining an index to local animal populations.

It has long been my opinion that many desert inhabiting animals, particularly volant forms, can readily be decoyed by smooth water-like surfaces even though these surfaces may be small in size. This was first brought to mind while observing desert bats attempting to water from the glistening and smooth but dry surface of an overturned water tank. A later observation furnishes further substantiating evidence for the foregoing opinion, and indicates again that even small water-like surfaces are investigated by numerous volant animals.

In September, 1947, A. C. Olson, K. Dixon, and I took a short trip to investigate a newly oiled section of Highway 78 in the Borego Desert, San Diego County, California. At the east end of the stretch of recently oiled surface

the tanker trucks had drained their oil residue at the roadside. The heavy crude oil had followed a shallow erosion gully for 100 feet into

TABLE I. *List of animals found in three small oil pools in Borego Desert, San Diego County, California*

| Animals trapped | No. counted |
|------------------------------|-------------|
| Insecta | |
| Orthoptera | |
| Grasshopper | 6 |
| Odonata | |
| Dragon fly | 5 |
| Damsel fly | 2 |
| Coleoptera | |
| Carabid beetle | 2 |
| Lepidoptera | |
| Butterflies (unidentified) | numerous |
| White-lined sphinx moth | 8 |
| Other moths (unidentified) | numerous |
| Reptilia | |
| Sauria | |
| Banded gecko | 3 |
| Brown-shouldered lizard | 1 |
| Aves | |
| Columbiformes | |
| Mourning dove | 2 |
| Passeriformes | |
| Orange-crowned warbler | 1 |
| Mammalia | |
| Chiroptera | |
| Desert little California bat | 1 |
| Other bats (unidentified) | 2 |
| Rodentia | |
| Bangs pocket mouse | 2 |

the desert. Three small connected pools had been formed; they varied from 2 feet to 14 feet in length, 1 foot to 4 feet in width, and $\frac{1}{2}$ inch to 1 inch in depth. This area is one of creosote bush desert, the soil is sandy and coarse, the weather is hot and dry, and there are few open watering places; the nearest being more than 5 miles away.

Trapped in the oil pools were numerous vertebrate and invertebrate animals. Among these were three bats, two mourning doves, one orange-crowned warbler, five dragon flies, and two damselflies, all of which, apparently, had been attracted by the water-like surfaces. Other animals (see complete list in table I) were also trapped during their nocturnal wanderings or while attempting to feed upon earlier victims, but probably they were not attracted by the water-like resemblance of the pools.

Unfortunately we were not able to search the entire roadside at the time when the oil was fresh. Nevertheless, the oil pools did reveal the fact that volant forms are attracted to small water-like surfaces.

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PHILIP H. KRUTZSCH

MUSEUM OF VERTEBRATE ZOOLOGY,
BERKELEY 4, CALIFORNIA

LARVAL COLEOPTERA AND DIPTERA FROM MARINE CRUSTACEANS

The gill chambers and egg masses of marine crustaceans, although providing shelter for nemerteans, copepods, cirripeds and other animals, are little known habitats for immature insects. Baylis ('15) found insect larvae in the gill chambers of two species of crabs, *Cardisoma hirtipes* Dana from the Admiralty Islands and *Gecarcinus landanii* (Milne-Edwards) from Christmas Island. These larvae were identified by Keilin ('21) as two species of cyclorrhaphous Diptera close to the family Ephyridae. Search of available indexes and literature indicates these to be the only published records of insect larvae from marine crustaceans.

Larvae of the genus *Wohlfahrtia* (Diptera: Sarcophagidae) have been found among the eggs on the swimmerets of *Sesarma dehaani* Milne-Edwards by Dr. A. S. Pearse of Duke University, who has permitted inclusion here of this previously unpublished data. The larvae were collected at Himejima-machi, near Osaka, Japan, on June 15, 1929.

Three species of insect larvae were collected from the gill chambers of crustaceans at Tarakan, Borneo, in August, 1945. The host crustaceans were found in a tidal marsh on the surface of moist mud. Dr. Wm. P. Hayes of the University of Illinois has kindly verified the Coleoptera mentioned below and Dr. O. A. Johannsen of Cornell University, the Diptera.

The first species is represented by four specimens of early instar larvae belonging to the family Dytiscidae (Coleoptera), taken from the gill chambers of a single female anomuran, *Thalassina anomala* (Herbst).

The second species includes eleven first instar larvae of the subfamily Chironominae, probably belonging to the genus *Chironomus* s.l. (Dip-

tera: Chironomidae). They were found in the gill chambers of two species of crabs, *Sesarma cumolpe* de Man and *Sesarma taeniolatum* White. These crabs run about on the surface of the mud and apparently habitually remain out of water for hours at a time.

The third species consists of two early instar larvae of the genus *Culicoides* (Diptera: Ceratopogonidae) from the gill chambers of *Sesarma cumolpe* de Man.

All six species of immature insects associated with crustaceans are from littoral or terrestrial hosts from the Pacific Ocean.

The relationships of the larval insects to the crustaceans are not clear. Both Baylis and Keilin (*loc. cit.*) believe that their larvae probably feed upon detritus or mucus in the gill chambers, but may be capable of piercing the gill surfaces. Since dytiscid larvae are known to feed upon copepods, their occurrence in the gill chambers of the anomuran may have been connected with the presence of copepods there (Humes, '47). Little can be said regarding the relationship of the *Culicoides* larvae to the crab. In the case of the *Chironomus* larvae, however, where specimens were taken from several crabs, it seems probable that the larvae live naturally in the gill chambers. Determination of the exact rôle of the insect larvae must await a study of the bionomics of both larvae and crustaceans.

At least four orders of insects (Collembola, Hemiptera, Coleoptera and Diptera) contain species which live either as immature forms or as adults in brackish or marine habitats. Only a few species have been found in association with marine crustaceans. Thorough investigation of the animals living on these crustaceans will probably bring to light other such insects.

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ARTHUR G. HUMES

DEPARTMENT OF BIOLOGY,
BOSTON UNIVERSITY

MESQUITE SEEDS REMAIN VIABLE AFTER 44 YEARS

Recently at the Southwestern Forest and Range Experiment Station five mesquite (*Prosopis velutina* Woot.) seeds were taken from a

herbarium specimen which was collected at Fort Lowell, Ariz., October 14, 1903, by Professor J. J. Thorner of the University of Arizona. Two of the seeds began to absorb water immediately when placed between wet cloths December 9, 1947, and one of the two germinated normally. Continuous wetting for six days produced no apparent change in the three remaining beans. Two of these seeds germinated readily after their impermeable coats were nicked with a file. Since three out of five seeds were viable (see fig. 1), proof is established that in the dry atmosphere of the herbarium, mesquite seed coats can retain their impermeability and embryos their viability for 44 years or more.

The practical implication of these results is that mesquite seedlings may be expected to appear on cleared lands for many years after eradication of the original stand even though transportation of new seed to the area by domestic livestock is prevented. Longevity of mesquite beans which are incorporated in the soil is further guaranteed by their hard impervious seed coats. In other germination tests, eight weeks of continuous wetting failed to penetrate the seed coats of 12 per cent of the viable mesquite seed from the 1946 crop. These seeds germinated immediately when their seed coats were notched through with a file.

S. CLARK MARTIN

SOUTHWESTERN FOREST AND RANGE
EXPERIMENT STATION,¹
TUCSON, ARIZONA

FIG. 1. Three seeds out of five taken from this 1903 herbarium sheet germinated 44 years later.

¹ Maintained by the Forest Service, U. S. Department of Agriculture, at Tucson, Ariz., and covering Arizona, New Mexico, and western Texas.

BOOK REVIEWS

A RUSSIAN TEXT OF ECOLOGY¹

This is the second edition of the posthumous work by Professor D. N. Kashkarov. The first edition was prepared for press by the author just at the outbreak of the war. At the beginning of the siege of Leningrad by the Germans, Professor Kashkarov was evacuated by plane and soon after died of a heart disease. The first edition of the book was published under the supervision of Professor P. V. Terentjev, who also edited the present, second edition.

The first chapter (38 pages) is devoted to a discussion of the subject matter and methods of animal ecology. The relation of ecology to other biological sciences, especially to general biology, is analyzed at length. Separate sections deal with the relations between ecology and biogeography, ecology and morphology, ecology and the science of behavior, ecology and paleontology, ecology and systematics, ecology and genetics. The importance of considering ecology as a science in its own right is emphasized everywhere. It is pointed out that the same problem may form the subject of a study in ecology or in some other science, depending on the emphasis on different aspects of the problem. For instance, the study of hibernation is a physiological problem if we study the effects of hibernation upon such functions as respiration, excretion, thermoregulation, etc. However, the study of hibernation becomes an ecological problem when we study such aspects as the relation between hibernation time and external environment, or study the adaptive rôle of hibernation.

In discussing the relation between ecology and genetics the author expresses the opinion that genetics hitherto developed without due consideration of the possible rôle of the environment. "Everything seemed to be fully included in chromosomes." The author rejects this point of view as "entirely wrong." He points out that what is inherited is not a given characteristic, but a predisposition to the development of that characteristic in a given environment. The author cites the work of Moshkovtzev which shows that in order for amphibians to develop legs it is necessary for tadpoles to swallow air. He points to the known experiments on *Proteus* which prove that light is necessary for the development of eyes. The author concludes that genetics and ecology must be closely related. He adds, however, "Of course not Morgan's 'gene' genetics."

Ecological methodology is discussed on pages 15-21. As an illustration of it, the work of Piatnitski (1935) on *Porthetria dispar* is described in some detail. That author studied various factors which are either beneficial or harmful to the insect. The beneficial factors are higher temperatures, lower humidity and younger forest trees. Other beneficial factors are the ease with which caterpillars are carried by wind, high production of eggs, and high sexual activity of the males. A harmful factor is the high reproduction rate which causes rapid overpopulation and results in a lack of food. By a proper control of such factors as the age of forest trees through a carefully planned forest conservation program, it is possible to successfully fight the insect.

The rôle of experiment in ecology is discussed and illustrated with a number of examples.

A rather large section (pp. 21-30) is devoted to the discussion of the importance of ecology in the economic development of the U.S.S.R. Problems of fisheries, crop yields, protection of plants, insect extermination, forestry, animal husbandry, and epidemiology are mentioned.

The chapter ends with a brief history of ecology. It is pointed out that in prerevolutionary Russia very little research was done in this field and that only in the last three decades did ecology flourish in the U.S.S.R.

The second chapter (100 pages) deals with environmental factors. Their effects are illustrated with numerous examples. Effects of temperature, humidity, light, precipitation, phenological and edaphic factors, and biotic factors are discussed by the author separately after a general survey.

After discussing the differences of optimal temperature ranges for different animals, the author describes the well known effects of temperature on locomotion, development, growth in plants, reproduction, etc. Many examples are illustrated by graphs taken from various sources. There is some confusion in the definition of the concept of "sum of heat." It is stated on page 49 that in ecology we may consider either the "sum of heat," expressed in gram-calories, or the temperature proper expressed in degrees. On page 56, however, we read, "If in a given locality the average monthly temperature is 20°, then for the summer period, from May to August, the sum of heat in that locality will be equal to 2440°." No reference is given on either page and this peculiar slip is rather puzzling.

In discussing the effects of temperature upon organic form the author mentions three laws:

¹ Kashkarov, D. N. 1944. Fundamentals of animal ecology. Leningrad. Pp. 383. Price: 20 rubles, 75 kopeks.

(1) the law of Bergman according to which mammals of closely related species are a larger size in northern regions than in southern regions; (2) the law of Allen which amplifies the law of Bergman and states that in mammals as well as in birds there is a tendency in colder regions of a reduction in the size of such parts as ears, tail and extremities because these parts dissipate considerable heat; (3) the law of Gloger states that dry hot weather favoring the formation of pheomelanins leads to a yellow, desert coloration whereas lower temperatures inhibit the formation of pheomelanins and result in the white coloration of arctic animals.

Effects of humidity as well as the combined effect of humidity and temperature are illustrated with several examples.

In the section on precipitation the author emphasizes the importance of climograms and refers to the work of Ball, Cook, Johnson and others. This section is illustrated by numerous curves. On page 87 the author speaks of an important improvement in the climographic method made by Uvarov ('32), but in the reviewer's opinion the presentation of Uvarov's method is not too clear and the reader would have to look up the original reference (in English).

The section on biotic factors (25 pages) discusses the rôle of food, the rôle of vegetation in animal life from the point of view of food and shelter, the effects of animals upon plants (rodents), mutual effects of animals. The notion of potential of reproduction is discussed.

The third chapter (12 pages) deals with a general description of the "stage of life," discussing the climatic and geographical zones.

The fourth chapter (27 pages) deals with adaptation in forms of life. Adaptation is illustrated with numerous examples ranging from insect larvae to birds. Protective coloration is discussed in a separate section.

The fifth chapter (36 pages) deals with acclimatization and the ecology of domestic animals. It begins with the statement of the importance of the theory of acclimatization for practical purposes and emphasizes the necessity of such studies for the economy of the U.S.S.R. References to several Russian authors are made (Maleef, Stanchevsky, Jitkov, Kashkarov). A brief discussion of Lamarckism is given and the latter is rejected as an explanation of acclimatization.

The ecology of domestic animals is illustrated by a brief survey of the ecology of the caracul sheep.

The sixth chapter (62 pages) deals with the notion of biocenosis. That notion is considered as one of the most important in ecology. It is

defined as "a complex of organisms, occupying a definite region in the stage of life." An oyster bed is given as an example. In general a biocenosis comprises different species of animals and plants. The cycle of different metabolic substances is discussed. It is pointed out that in American literature the word "community" is used in the same sense as biocenosis. The word "community" is also used occasionally in Russian literature. The author, however, considers the word "community" as being anthropomorphic and as implying some "social relations" between individuals. Such social relations, according to the author, do not and cannot exist in the plant or animal world. The interactions in a biocenosis are of a different nature. Limits of stability and the ecology of biocenosis are discussed. This is followed by a discussion of the structure or morphology of biocenosis and concluded with a section on the dynamics of biocenosis. Fluctuation in the numbers of individuals of a species are illustrated with several examples. The chapter ends with a discussion of ecological successions.

The seventh chapter (36 pages) deals with ecology and evolution. In discussing the struggle for existence, mention is made of V. Volterra's mathematical work and of Gause's experiments which reproduced periodic fluctuations of two species (predator and prey) with *Paramecium aurelia* and *Saccharomyces exiguus*. The author's general attitude toward elaborate mathematical studies is negative.

The eighth chapter (20 pages) discusses quantitative measurements in ecology. A number of Russian and foreign authors are cited.

Finally the ninth chapter (25 pages) gives an example of an ecological study by discussing the ecology of the desert. A number of illustrative data on the soil, flora and fauna of the deserts of Soviet Central Asia is given. The book ends with a bibliography in the Russian language and in foreign languages. The list of publications in Russian contains about 400 titles, the list of publications in foreign languages contains about 500 titles. The lack of an index very much reduces the value of this book as a reference work. The book contains 163 illustrations and graphs.

From our American point of view the paper and printing are decidedly poor. Remembering, however, that the book was published at the peak of Russia's struggle with Germany and that two editions appeared between 1941 and 1944, the reviewer is more inclined to a feeling of amazement than of criticism.

N. RASHEVSKY

THE UNIVERSITY OF CHICAGO,
CHICAGO, ILLINOIS

HORMONES AND BEHAVIOR¹

Dr. Frank Beach, one of the leaders in the study of behavior at the present time and an able exponent of the analytical aspects of behavior, particularly as it has definite relations to the functions of internal secretory organs, has rendered a signal service to all those interested in biological mechanisms and particularly to those who are more interested in behavioral aspects of life. He has assembled and skillfully arranged a wide coverage of the literature with the view of integrating the known facts and introducing the many special problems with those findings which are available in the literature, albeit they may be few in many instances. It is a commendable attempt to organize the literature in a logical manner and to present the conclusions of various investigators, and, although handled with critical judgment, it is by no means an evaluation of the findings of others. The reader is invited to aid in the evaluation of the many suggested influences that are attributed to the endocrine secretions.

From the literature of the world, including the many publications of the author himself, some 700 to 800 articles provide the main substance for this well integrated treatise. Owing to the relatively recent upsurge in studies of the organs of internal secretion, stimulated by the availability of some chemically pure hormones, it is understandable that only about one per cent or less of the literature cited was published prior to 1920 and that approximately 50 per cent of it has appeared in print during the period 1940 to 1946. The currency of the majority of the papers cited is thus obvious.

The foreword by Dr. Earl T. Engle, Chairman of the Publications Committee of the Association for the Study of Internal Secretions, states, "It will be a book of constant reference for physiologists and psychiatrists, for zoologists and sociologists, and for all those who are interested in deriving from animal experiments the basic principles to be used in some future comprehensive analysis of human behavior."

In the preface the author defines as his goal "the collection of as representative as possible a cross section of published experiments and observations dealing with relations between hormones and behavior." The rôle of the book "is not the exposition of a thesis, but the supplying of a book of facts and references." The materials have been organized in terms of general categories of behavior, and whereas considerable attention is given to the morphological aspects of endocrinology, it is only because certain special structures have a bearing on the

problems of behavior. The book is composed of 14 chapters, and in addition to the bibliography citing author, full title and reference, a glossary of 8 pages enables an average reader to comprehend easily the technical terms; a 12-page index is valuable. Whereas the general scope is largely restricted to the vertebrate animals, of all classes from fishes to man, some references are also given to observations on invertebrates.

The first chapter, on courtship and mating, attempts to correlate the condition of the endocrine organs, more especially the gonads, with the various types of behavior; gonadal cycles, removal of gonads, injection of hormones, induction of unusual cycles, constitute variable conditions that become apparent in modified courtship and mating behavior of vertebrates of all classes. Effects of other than gonadal hormones are likewise reviewed. Chapter II deals with the reversal of behavior in untreated animals, behavioral phenomena encountered in spontaneous alteration of the gonads, after gonad transplantation, after administration of hormones of the homologous as well as heterologous sex, and the atypical pattern of human homosexuality serve to emphasize the bisexual potentialities existent in animals of all vertebrate classes. Facts portrayed by such a review immediately call into question a somewhat prevalent notion of the specificity of a given sex hormone and emphasize the many possible varieties of behavior that may be elicited by the same endocrine substance in animals of different genetic sexuality. "All in all there has been an unfortunate tendency to place an oversimplified interpretation on behavior changes consequent to experimental manipulation of the gonadal hormones." In Chapter III the review concerns itself with the literature bearing on the influence of hormones on preparation for production and care of young. Oviposition and care of eggs in fishes and amphibia, nesting and care of young in birds, parturition and parental responses to young among mammals are complex behavior patterns that are influenced by internal secretions. Chapter IV reviews the present notions of the influence on migration of birds whereas Chapter V treats of such hormonally conditioned activities as generalized aggression, social dominance, and territorial defense. Chapter VI, on the relation of hormones to emotions, refers to lower animals as well as to man. In Chapter VII, treating the relation of hormones from the different organs of internal secretion to conditioned reflexes and other types of learning, one finds collected the literature that is at least suggestive for the problem if not wholly satisfactory; it does serve to point the way to the study of many unsolved problems. Chapter VIII concerns itself with the influence of endocrine secre-

¹ Beach, Frank A. 1948. *Hormones and behavior*. A survey of interrelationships between endocrine secretions and patterns of overt response. N. Y.: Paul B. Hoeber, Inc. Pp. 382. \$6.50.

tions on the amount and character of general body activity displayed by animals of the vertebrate groups. In Chapter IX is included the literature relating to an analysis of the internal economy of the organism or homeostasis, general metabolism, metamorphosis and moulting, as these may be modified or partially controlled by hormones. Chapter X is concerned with the hormonal basis for development of many external morphological structures that may affect behavior even though somewhat indirectly; these secondary sex characters, ranging from coloration or excrescences in fish to the general condition of the genital organs of man, are reviewed primarily in the rôle of modifiers of behavior and do not involve exhaustive morphological description. Chapter XI, on the rôle of nervous stimulation, discusses the manner in which functions of the endocrine organs are affected or controlled by external stimulation. Stimuli are divided into the two classes of general environmental characteristics—temperature, humidity, illumination—and such psychological stimuli as may emanate from another animal or its general behavior. Chapter XII, under the title "Developmental Aspects," directs attention to the gradual appearance of hormone effects during ontogeny. Puberty and sexual maturation are progressive phenomena dependent upon such elements as the beginning production of hormones by the organs concerned; the release of the hormones into effective relations with the whole organism; the establishment of sensitivity on the part of the end organ or tissues to the hormones, and the capabilities of precocious development from artificial applications of hormones or from pathological conditions involving hormone secretion. The establishment of sufficiently developed neuromuscular organization that enable responses to hormones are also elements for consideration. Chapter XIII is an enlightened critique in which the literature is assembled to point out some of the complexities in interpretation of

hormone effects. It focuses attention on the major sources of variability and emphasizes that a specific behavior may not depend upon the chemical constitution of the hormone. Variable effects may be obtained from the use of the same pure chemical substance on account of such factors as the age of the animal when treated, its genetic sex, conditions at the time of treatment, external or internal stimulation, previous hormonal treatment, species or individual differences. In Chapter XIV, which concludes the review of the literature bearing on the rôle of hormones in conditioning behavior, the author turns attention to a review of the more general theories and interpretations of hormonal effects. Some of the difficulties inherent in the analysis of behavior are carefully pointed out. Guiding principles and generalizations are suggested, and discussions of how the hormones mediate a particular type of behavior come in for attention. The manner in which hormones cooperate with or supplement the neuromuscular organization to effect behavior is obviously a central problem.

The organization of the vast amount of material available is purposeful and acceptable; it could have been arranged in many different ways but any organization would have involved some repetition of reference to the same study. To have organized and to have even partially digested the vast number of papers on the subject is a huge task and a service of great value to those interested. It provides a framework of analysis that cannot but stimulate further efforts to make our knowledge more complete in these areas. The book has great value for those attempting to explore the biology of the endocrine glands or to those whose interest directs attempts toward an understanding of behavior or its basic instigation.

CARL R. MOORE

HULL ZOÖLOGICAL LABORATORY
THE UNIVERSITY OF CHICAGO

SCIENTISTS STARRED, 1903-1943¹

This massive book deals in elaborate detail with all aspects of starring the leading scientists in the various editions of "American Men of Science." Approximately 2600 persons have been starred in these volumes.

The author, a professor of geography in Indiana University, has been keenly interested in the subject matter of this book since the first edition of "American Men of Science" appeared in 1903 and has written a number of articles on the same general subject.

In a review of this scope it would be out of

place to deal with the origin and history of "American Men of Science," the well-known bibliographic directory edited and published by the late McKeen Cattell. Suffice it to say that Cattell introduced for the first time a scheme for ranking scientists according to their merit. He asked ten outstanding leaders in twelve sciences to list in the order of merit the leading research scientists in their fields. From these lists he worked out the average rank of each man voted upon, and in the first edition of A. M. of S. 1000 persons were starred out of some 4000 written up in the book. As time went on all previously starred persons were allowed to vote for additional candidates for starring in subsequent editions.

¹ Stephen Sargent Visser. 1947. Scientists starred 1903-1943 in "American Men of Science." The Johns Hopkins Press, Baltimore, Md. 556 pp., 117 figures.

The significance and value of starring individuals has met with varied reactions. As might be expected, some were favorable and some were unfavorable. In the present volume Professor Visser has thoroughly canvassed the matter and on the whole has passed favorable judgment on its usefulness and value to science. He seems to think that in later editions of *A. M. of S.* the starring has become progressively more and more fair and democratic. Also more and more sub-sciences and border-line fields have been included which were not represented in Cattell's original arbitrarily selected twelve sciences. Starring scientists solely on the basis of research, without considering effectiveness in teaching, has been severely criticized and this injustice is partly compensated by listing a number of outstanding teachers.

In the present volume is presented a geographic, demographic, sociologic and genetic study of starred scientists based on information derived from the sketches of scientists in *A. M. of S.*, their sketches in "Who's Who in America," extensive questionnaires sent to all starred scientists and personal interviews with many representative scientists. Their education and other background influences are studied, graphed and analyzed for each of the listed departments of science. Their places of birth, collegiate and graduate training, and place of employment are given. The starred alumni of each of the colleges and universities are listed by departments of science and year of graduation. Lists are given of some starred scientists who have been especially effective as teachers, the starred women, starred fathers and sons, starred brothers, and (for the first 1000 starred in 1903) their order of eminence in their chosen fields.

This study of 2607 starred scientists was made with four chief objectives: "(1) To find out where these leaders in American science were born, educated and employed. (2) To discover what conditions correlate with their production. (3) To ascertain what can be learned from them or otherwise as to possible methods of increasing the number of such outstanding workers and of increasing scientific achievement. (4) To provide supplementary recognition of the contribution made by these scientists and

thus to encourage those who are living and honor those who have died."

Some of the general conclusions derived from these studies of starred scientists may be briefly set down as follows:

1. "Notable persons are a product of both environment and heredity, certainly not predominantly one of these."
2. The influence of home and community is of prime importance.
3. A favorable climate is necessary for the exercise of energy and ambition.
4. Superior teachers in high school and college stimulated interest and ambition in those who were starred.
5. Young and vigorous college and university presidents are distinctly advantageous in promoting research and effective teaching.
6. Among the requisites for success in scientific research are curiosity, perseverance and enthusiasm. Personal attractiveness and superior memory are much less essential.
7. Starring scientists in 'American Men of Science' is regarded as a stimulating and encouraging factor in successful research."

Most of these conclusions and suggestions are in agreement with current thought and need no comment. Any further attempt to report the contents of this book would lead into discussions too numerous for the present reviewer to undertake.

One aspect of the book, however, that will undoubtedly gain much publicity is that which ranks universities in the order of the scientific standing of their various departments, based on the starring of men on their faculties and their ranking in the estimation of their colleagues.

For starred scientist themselves it may perhaps be of interest to find their names listed in a number of different categories with information as to their academic training and the edition of *A. M. of S.* in which they were first starred. As a book of record and reference this volume will doubtless be a must for most libraries, but as reading material for the average scientist, starred or not, it cannot be very heartily recommended.

H. H. NEWMAN

PLANTS AND ENVIRONMENT¹

There long has been a need for a greater choice of textbooks in the teaching of plant ecology. Daubenmire's recent text is a welcome addition to the field. The greater part of the book is devoted to description and analysis of

¹ Daubenmire, R. F. 1947. *Plants and environment: a textbook of plant autecology*. N. Y.: John Wiley & Sons, Inc. xii + 424 pp.; 87 figs. \$4.50.

the physical environment. Interpolated in the discussion of the environmental factors are interpretations of the physiologic and morphologic response of the plant to these factors and many examples of plant-environmental interrelationships. The contents are based on the premise that plant ecology can be adequately treated in two separate phases, namely autecology and synecology. Daubenmire states that a knowl-

edge of the ecology of the individual plant is necessary to understand the structure of the plant community. This may be true in part, but much autecology has been learned by studying synecology. Often the ecology of the individual species is best expressed by its relationships to other species of the community. Too sharp a divorce between autecology and synecology tends to limit the viewpoint in ecology. In the reviewer's opinion, Daubenmire might have strengthened the presentation of autecological concepts by including synecological applications and examples.

The chapter topics are comprehensive and in logical order. They include the soil, water, temperature, light, atmosphere, biotic and fire factors, and the environmental complex and ecologic adaptation and evolution. Treatment of the fire factor as a specific part of the environment is unusual, but satisfactory. The whole sequence of topics has a certain amount of integration and dependent continuity which is necessary in a discussion of such a broad field of science.

The book is well written, with clear concise language, and not overburdened with terminology. The student should readily comprehend the principles and facts that are presented and associate them with the plant as a living organism. The book is especially unique in that it supplies the student with a background of the pertinent principles of geology, chemistry, physics, meteorology, etc., necessary in understanding the environmental relationships of the plant. This saves the student and instructor time, while a representative bibliography provides the student with the source of data if a more detailed and critical examination of the research is needed. In some chapters, however, discussion of the factors and processes responsible for the physical environment is too lengthy and detailed and with little or at best only a remote connection with ecology. Several pages devoted to a discussion of the transport of the parent materials of soil seems superfluous, especially when this subject is treated in general terms with few specific applications of plant ecology. In the chapter on the water factor, considerable space is devoted to purely meteorological processes and factors which have no direct pertinence to the plant. Some of this discussion is elementary and the principles discussed certainly are well recognized by the average college student.

Whereas most of the text concerns the environment and the immediate response of the plant to it, the last chapter deals with the long range response as expressed through adaptation and evolution. This chapter is concerned with some of the causes and methods of individual changes in relation to the environment. Tureson's genecologic classification is interpreted and some of its aspects applied to autecology. The concept of teleology is discussed and shown

to be untenable so far as autecology is concerned. It is interesting to note, however, that although Daubenmire explains the fallacy of teleology, there are statements in the text with teleological implication, merely emphasizing the fact that it is often difficult to speak of plant growth, movements, and reactions without inadvertently having a teleological slant.

There seem to be few technical errors. Under the topic of "soil moisture" the fraction for determination of the volume weight is inverted. The dry weight in grams should be divided by the natural volume. "Volume weight" might better be called "weight-volume ratio." Another statement that is open to question is that hydrophytes include bog plants. This does not take into consideration the physiological aspects of bog water, which is too cold and acid to permit unlimited intake by all plants. Many of the ericaceous bog plants thrive on dry soil. The reviewer has collected *Ledum groenlandicum* and other ericads on dry, west-exposed, sandstone cliffs in the Driftless Area of Wisconsin, while they were entirely absent in a tamarack swamp a few hundred yards from the base of the cliff. The occurrence of *Ledum* and *Vaccinium* on dry, sandy soils adjacent to muskegs in northern British Columbia and Alberta does not indicate a hydric nature.

Autecological concepts and principles are rather hard to illustrate by photography, but Daubenmire has assembled a series of photographs that illustrate certain of his points. A greater number of pictures could be included to advantage, but careful selection of a limited number is more essential, unless they are exceptionally good.

There are few typographical and mechanical errors. The only one noted of significance is a page of discussion under "multiplicity of factors" exactly duplicated under "dynamic nature of environment."

The book is written in a scholarly manner, the field is well covered, the facts are accurately presented, and the application of the principles is comprehensive. It will serve its purpose well, namely, as a textbook for a course in plant autecology or that portion of general ecology dealing with autecology. It is the reviewer's opinion, however, that an elementary course in plant ecology, which presents the principles of this important phase of botany, should include both autecology and synecology. Without a proper balance between these two, which can hardly be realized when treated separately, it does not seem possible to present a complete and coordinate picture of plant ecology, either as a terminal course or to the beginning ecologist.

H. P. HANSEN

DEPARTMENT OF BOTANY,
OREGON STATE COLLEGE,
CORVALLIS, OREGON

PLANTS AND PLANT SCIENCE IN LATIN AMERICA¹

Frans Verdoorn, editor of this fascinating *omnium gatherum*, has, in its preparation, enlisted the cooperation of many distinguished South American and North American collaborators. However, in its use the reader should keep in mind the editor's wise warning at the beginning of the Table of Contents (which is at the back of the volume)—"As it was not feasible to prepare a subject index for our polyglot volume, it is important that every reader examine this table of contents with some care! It contains in Part I cross-references to Part II and vice versa." This warning is necessary, for if the reader sets out to obtain specific information by the simple expedient of leafing through the pages in the expectation of an alphabetical arrangement, he will be disappointed. He must consult the table of contents unless he wishes to become engrossed in a totally different subject, sometimes set forth in English, sometimes in Spanish, Portuguese or French. Under any circumstances the reader may be waylaid by the abundance of fascinating and definitely worthwhile illustrations, which suggest sources of teaching material or of original information often unknown or perhaps long forgotten.

General background information significant to the ecologist is to be found in several articles on geology, climate and soils. The geology of Latin America is treated briefly by W. C. Darrah in two articles, one on the Antilles and Central America, the other on South America. Climatology and meteorology are critically presented by R. G. Stone. Soils are discussed in two articles, "Some important soils of Central America" by R. L. Pendleton, and "The soils of South America" by F. Hardy.

For a broad phytogeographic treatment of plant groups the reader will turn to A. C. Smith and I. M. Johnston, "A phytogeographical sketch of Latin America," well illustrated with a double-page map and selected photographs and line drawings. Reference should also be made to E. Rausz's decorative end papers and to Plate 36 (Agricultural regions of South America). From this point on, the more detailed descriptions of the plant cover of Latin America largely follow political lines. Cultivated plants are treated in articles which usually include "Natural resources" in their titles, and discussions of native vegetation usually fall under "The vegetation of . . .," although ex-

ceptions are to be found. Nor should the articles on forest and agricultural conditions in the country of interest be ignored. Of course the indispensable "Table of Contents" must be assiduously consulted in any organized plan of reading. By and large, it is possible to obtain an excellent picture of the extent of floristic and, to a lesser degree, of ecological knowledge of the Americas south of the Rio Grande. It is not to be expected that there would be uniformity of treatment of ecological matters in a work essentially encyclopedic in plan, nor will the reader be disappointed in this respect—he will find stimulating variety here!

The conversationist will find much of value in H. J. Coolidge's "Notes on conservation in the Americas," as well as in scattered articles throughout, perhaps especially those on forest resources.

Careful search will yield information to those who have an especial penchant for the relations between man and his plant environment, starting with A. F. Hill's "Ethnobotany in Latin America" and branching out into some of the detailed aspects of man's use of plants.

Of value to all botanists are a series of general articles—"Historical sketch" by F. W. Pennell; "The advantages of the tropical environment for studies of the species problem" by Marston Bates; "Agricultural scholarships and inter-American relations" by K. A. Ryerson; "Some of the principal Latin American plant science periodicals" by Paul L. Guest; "Plant science institutions, stations, museums, gardens, societies and commissions in Central and South America" by Frans and J. G. Verdoorn, and the "Introductory bibliographical notes, 1 and 2" by the editor.

Certainly no botanist should miss reading Verdoorn's provocative introductory essay, "The plant scientist in the world's turmoils." While one may not agree completely with this essay in detail, its general tenor must be taken seriously—and, it is to be hoped—acted upon.

Verdoorn is again to be congratulated on an enterprise in botanical publishing which, on this occasion, is of double benefit—to the research worker-teacher in his immediate pursuits—and in the cementing of hemispheric good will among plant scientists. It is, however, devoutly to be hoped that the philanthropic editor-publisher will ultimately re-issue this compendium in a revised and more usable form. As it stands it should nevertheless be at the right hand of every internationally-minded botanist.

ERNST C. ABBE

DEPARTMENT OF BOTANY,
UNIVERSITY OF MINNESOTA

¹ Frans Verdoorn, editor. 1945. Plants and plant science in Latin America. Waltham, Mass.: the Chronica Botanica Co.; New York City: G. E. Stechert & Co. Pp. xxxv + 384. \$6.00.

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Catastrophic Mass Mortality of Marine Animals and Coincident Phytoplankton Bloom
on the West Coast of Florida, November, 1946 to May, 1947.

GORDON GUNTER, ROBERT H. WILLIAMS, CHARLES C. DAVIS AND F. G. WALTON SMITH

The Vegetation of Western Cross Timbers.....E. J. DYKSTERHUIS

An Ecological Study of Snails of the Genus *Busycon* at Beaufort, North Carolina.
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VOL. 29, No. 4

CONTENTS

OCTOBER, 1948

| | | |
|---|-------------------------------------|-----|
| Variations in size and composition of fish populations in recently stocked ponds | LOUIS A. KRUMHOLZ | 401 |
| Plant communities in the vicinity of the volcano El Parícutin, Mexico, after two and a half years of eruption | WILLIS A. EGGLER | 415 |
| The survival of wild brown rats on a Maryland farm | DAVID E. DAVIS | 437 |
| Grassland types of south central Montana | JOHN C. WRIGHT AND ELMORA A. WRIGHT | 449 |
| Ecological segregation of inter-fertile species of <i>Colias</i> | WILLIAM HOVANITZ | 461 |
| Terron vegetation in New Mexico | ALTON A. LINDSEY | 470 |
| Observations on a population of the salamander, <i>Amphiuma tridactylum</i> Cuvier | FRED R. CAGLE | 479 |
| Palynological studies at Sodon Lake, Michigan. Part III. The sequence of pollen spectra, Profile I | STANLEY A. CAIN AND J. V. SLATER | 492 |
| Notes and Comment: | | |
| Temporary changes of certain limnological conditions in western Lake Erie produced by a windstorm | TED F. ANDREWS | 501 |
| Observations on the effect of flood on animals | LUCILLE F. STICKEL | 505 |
| Fog and atmospheric carbon dioxide as related to apparent photosynthetic rate of some broadleaf evergreens | C. C. WILSON | 507 |
| Plant succession on fallen logs in a virgin spruce-fir forest | HERBERT A. MCCULLOUGH | 508 |
| A new vegetation map of Manchuria | A. W. KÜCHLER | 513 |
| The use of the punched card method in phytosociological research | GRANT COTTAM AND J. T. CURTIS | 516 |
| A range society formed | HAROLD F. HEADY | 519 |
| Book Reviews: | | |
| Merrilleana (Verdoorn) | E. C. ARBE | 521 |
| A sociologist looks at the "Kinsey Report" (Kinsey, Pomeroy, Martin) | HERBERT BLUMER | 522 |
| Conservation in the United States (Gustafson et al.) | CURTIS L. NEWCOMBE | 524 |
| Mammals of Washington State (Dalquest) | C. C. SANBORN | 525 |
| Index to Volume 29 | | 527 |

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Vol. 36, No. 1

Contents

July 1948

TROPICAL SOIL-VEGETATION CATENAS AND MOSAICS. A STUDY
IN THE SOUTH-WESTERN PART OF THE ANGLO-EGYPTIAN SUDAN. BY
C. G. T. MORISON, A. C. HOYLE AND J. F. HOPE-SIMPSON.

AN INDEX FOR ESTABLISHING THE DEGREE OF MATURITY IN
PLANT COMMUNITIES. BY DR. RODOLFO E. PICHI-SERMOLLI.

THE EFFECT OF ARCTIC AND HIGH MOUNTAIN CLIMATES ON
THE CARBOHYDRATE CONTENT OF *OXYRIA DIGYNA*. BY
R. SCOTT RUSSELL.

STAGES IN INVASION AND REPLACEMENT DEMONSTRATED BY
SPECIES OF *MELANDRIUM*. BY H. G. BAKER.

A SURVEY OF THE ROCKLAND-CLAXTON LEVEL, NORFOLK.
BY J. M. LAMBERT.

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| | |
|---|-----------------------------|
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TABLE OF CONTENTS, VOLUME 29, 1948

| | |
|--|-----|
| Changes in vegetation and production of forage resulting from grazing lowland prairie. J. E. WEAVER AND R. W. DARLAND | 1 |
| Method in ecology—Biapocrisis. A. G. HUNTSMAN | 30 |
| Water relations of the Polypody fern, <i>Polypodium polypodioides</i> (L.) A. S. Hitchcock. ROBERTA POTTS AND WM. T. PENFOUND | 43 |
| The nutritional value of marine zooplankton with a consideration of its use as an emergency food. GEORGE L. CLARKE AND DAVID W. BISHOP | 54 |
| Annual-plant vegetation of the California foothills as related to range management. J. R. BENTLEY AND M. W. TALBOT | 72 |
| The fat content of a butterfly, <i>Danaus plexippus</i> Linn., as affected by migration. GEOFFREY BEALL | 80 |
| Some effects of algae and molds in the rain-crust of desert soils. JOEL E. FLETCHER AND W. P. MARTIN | 95 |
| Bird populations and biotic communities in Northern Lower Michigan. S. CHARLES KENDEIGH | 101 |
| The rate of recovery of decimated populations of brown rats in nature. JOHN T. EMLER, JR., A. W. STOKES, AND C. P. WINSOR | 133 |
| Postglacial forests of the Glacier National Park region. HENRY P. HANSEN . | 146 |
| The seasonal occurrence of sedentary marine organisms in Biscayne Bay, Florida. CHARLES M. WEISS | 153 |
| Relation of soils and forest growth in the driftless area of southwestern Wisconsin. S. A. WILDE, PHILIP B. WHITFORD, AND C. T. YOUNGBERG ... | 173 |
| Modal temperatures for the greenhouse whitefly <i>Trialeurodes vaporariorum</i> and its parasite <i>Encarsia formosa</i> . THOMAS BURNETT | 181 |
| Perennial grass composition as an indicator of condition of southwestern mixed grass ranges. R. H. CANFIELD | 190 |
| Some conversational autobiographical notes on intellectual experiences and development: an auto-obituary. BURTON E. LIVINGSTON | 227 |
| Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. F. W. WENT | 242 |
| The commonness, and rarity, of species. F. W. PRESTON | 254 |
| A contribution to the knowledge of the Pleistocene flora of Minnesota. C. O. ROSENDAHL | 284 |
| A comparison of two ants of the genus <i>Formica</i> . MARY TALBOT | 316 |
| Forest sequence and climatic change in northeastern North America since early Wisconsin time. PAUL B. SEARS | 326 |
| The ecological succession of spiders of the Chicago area dunes. D. C. LOWRIE | 334 |
| Life-form spectra of the hardwood forests of the Itasca Park region, Minnesota. MURRAY F. BUELL AND ROBERT L. WILBUR | 352 |
| Toleration of lowered oxygen tension by cave and stream crayfish. W. D. BURBANCK, JOHN P. EDWARDS, AND MADELINE P. BURBANCK | 360 |
| The fecundity and development of the flour beetles, <i>Tribolium confusum</i> and <i>Tribolium castaneum</i> , at three constant temperatures. THOMAS PARK AND MARIAN BURTON FRANK | 368 |

| | |
|---|-----|
| Variations in size and composition of fish populations in recently stocked ponds. LOUIS A. KRUMHOLZ | 401 |
| Plant communities in the vicinity of the volcano El Parícutin, Mexico, after two and a half years of eruption. WILLIS A. EGGLER | 415 |
| The survival of wild brown rats on a Maryland farm. DAVID E. DAVIS | 437 |
| Grassland types of south central Montana. JOHN C. WRIGHT AND ELNORA A. WRIGHT | 449 |
| Ecological segregation of inter-fertile species of <i>Colias</i> . WILLIAM HOVANITZ | 461 |
| Terron vegetation in New Mexico. ALTON A. LINDSEY | 470 |
| Observations on a population of the salamander, <i>Amphiuma tridactylum</i> Cu- vier. FRED R. CAGLE | 479 |
| Palynological studies at Sodon Lake, Michigan. Part III. The sequence of pollen spectra, Profile I. STANLEY A. CAIN AND J. V. SLATER | 492 |
| Index to Volume 29 | 527 |
| Notes and Comment, 115, 116, 120, 121, 123, 124, 125, 205, 208, 209, 215, 375, 376, 382, 386, 389, 391, 392, 393, 501, 505, 507, 508, 513, 516, 519. | |
| Book Reviews, 127, 128, 129, 130, 219, 221, 222, 223, 394, 396, 397, 398, 400, 521, 522, 524, 525. | |
| Book Notices, 131, 225. | |

ECOLOGY

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No. 4

VARIATIONS IN SIZE AND COMPOSITION OF FISH POPULATIONS IN RECENTLY STOCKED PONDS *

LOUIS A. KRUMHOLZ

Department of Zoology, Indiana University

INTRODUCTION

During the past decade or so fisheries biologists have used various terms when referring to the total weight of a fish population. Among those so used, productivity, fish production, carrying capacity, standing crops, yield and others have been prominent in the literature. In some instances terms which should imply different aspects of the dynamics of the population have been used synonymously. In others, obscure meanings have been inferred that have further confused an already difficult picture. More recently Clarke ('46) included ". . . All the ideas and measurements of productivity which have an ecological application, . . . under the following three fundamental concepts . . ." (1) standing crop, (2) material removed, and (3) production rate. For purposes of the present and related work the following definitions are proposed:

1. *Productivity and production.* The word productivity should be used as a general term following the proposal of Clarke. There it embraces all the concepts of the dynamics of production. Productivity is not merely the rate of production of organic material in a body of water as suggested by Riley ('40) and Lindeman ('41, '42). Rather, the rate of production is only one phase of productivity as outlined by Clarke. Further, Clarke wrote (p. 324) ". . . To avoid

ambiguity in discussing the ecological relationships of the area, it is suggested that the terms 'productivity' and 'production' be not used in referring to the standing crop or to the material removed unless a phrase is added to make the meaning clear (Ivlev, '45). . . ."

Production is used by Clarke in a more exact sense than is productivity, and several varieties or quantitative aspects of production are distinguished. The most useful of these is the net or true production, which, as it applies to fish populations, is the total amount of fish body substance produced during a given period of time, regardless of whether or not it survives to the end of that time. Ricker ('46) outlined a method of determining the production of a population on the basis of its rate of growth and rate of mortality.

This use of the word production by Clarke and Ricker was unavoidable because of the lack of any other English word for the concept involved, and it has the less important virtue of being etymologically primitive. However, it is likely that the word production will also continue to be used in the various other senses described below.

2. *Carrying capacity.* Apparently this term was borrowed from the game biologists, who, in terms of game animals, use it to indicate the maximum density of a species that any range is capable of supporting without deterioration of that range (Leopold, '39). By analogy, in fish pop-

* Contribution No. 385 from the Department of Zoology, Indiana University.

ulations the same term should signify the upper limit of the weight of a species or combination of species that can be supported by a body of water over an extended period of time. Here, however, deterioration in the population itself, through overcrowding and consequent stunting, is a better indication that the carrying capacity has at least been reached than is any noticeable deterioration in the environment.

There is thought to be a direct correlation between the carrying capacity of a body of water and the fertility of the soil in which it is located. Ponds in the fertile prairie land of Illinois and Iowa are generally capable of supporting more pounds of fish per acre than are ponds in the relatively infertile soils of Alabama or Texas. Fertilizers, when properly applied to soils, will alter the productivity of land to a remarkable degree. If the fertilizer is applied but once the effect is temporary. To obtain a sustained alteration, repeated applications of fertilizer must be made. Waters respond similarly to fertilization. Alterations in the productivity and carrying capacity of a pond may be brought about either directly by applying fertilizer to the pond or indirectly by fertilizing the watershed.

There is evidence that there may be considerable difference in the carrying capacity of a body of water depending on the kinds of fish present. If carp is the dominant species, the carrying capacity in pounds of fish per acre is likely to be greater than if bluegills are dominant. Similarly, the capacity for bluegills will be greater than that for largemouth black bass. Such differences in carrying capacity are linked directly with the lengths of the food chain supplying the dominant species (Thompson, '41; Ivlev, '45), so that the species composition of the population may affect the carrying capacity. Further, there is evidence (Trautman, '41; Swingle and Smith, '41; Bennett, '43, '44) that the species composition of a fish population may oscillate back and forth with one species becoming dominant at

the expense of another and vice versa. Based on these criteria it seems reasonable to conclude that the carrying capacity of any body of water will change from time to time if there is a change in fertility or if there is any marked shift in composition between species utilizing different food chains.

The weight of the total population present is not necessarily an indication of the carrying capacity of a body of water. In some cases the carrying capacity of a body of water is not reached because of excessive exploitation (Bennett, '45), or that capacity may conceivably be temporarily exceeded, as suggested by the data of Eschmeyer ('37), Ricker ('42), and others. In the latter instance the fish population would have increased rapidly up to a point where the food supply became reduced because of too great consumption. Then the ability of the lake to produce food would suffer because of the overabundance of fish. At this reduced level of food production the population would be unable to maintain itself and would decrease in bulk as a result of cannibalism, a decreased rate of reproduction, and/or a loss in weight of the individual fishes which make up the population. If these processes are sufficiently severe, they may reduce the stock to a point where food production may again increase, but it is also possible that the population will be maintained at a level which, although lower than the peak, would continuously restrict the production of food and the fish population of the lake below its carrying capacity.

Although the term carrying capacity may represent a useful theoretical concept, I know of no body of water for which that capacity has actually been determined.

3. *Standing crop.* Here, again, Clarke's concept is followed. The standing crop (biomass) is the total weight of all the fishes present in the area at the time of observation. Further, Clarke ('46:324) wrote, "... the magnitude of the standing crop cannot be taken as a measure of the rate of production, just as the level of

water in a tank gives no clue as to the rates of inflow and outflow. . . ."

The standing crop is not necessarily a measure of carrying capacity. It has been pointed out that the carrying capacity is the upper limit of weight that can be supported by a body of water whereas the standing crop is the total weight present at any moment. If the body of water in question is supporting its maximum weight of fish then the standing crop is a measurement of the carrying capacity, otherwise not. Just as the carrying capacity may vary from time to time so also may the standing crop. We know that there are not the same numbers of rabbits, pheasants, quail, or of non-game birds and mammals in the same area year after year. Such populations are affected by changes in environment that may cause the population to increase or decrease, or they may vary in response to some type of internal population dynamics. Further, the numbers of game animals and birds may be drastically reduced by hunters. It seems unreasonable to believe that fish react any differently to changes in their environment and every time a fisherman angles successfully there is a decrease in the total amount of the fish that remain.

4. *Yield.* When speaking of fish populations the yield is the weight of fish removed during a stated period of time. It is the crop that is harvested and corresponds with Clarke's "material removed." Many workers have used production synonymously with yield. For example, Thompson ('41:206) wrote ". . . The term 'production' as used in connection with fish signifies the yield—the crop that is harvested. . . ."

In warm-water fish culture the total population of a pond at the end of a summer is commonly removed and either eaten or distributed elsewhere. In that case the yield of the pond for the year is the same as the standing crop at the close of the growing season. This final standing crop or yield is what has been called production by Meehan ('33, '34), Langlois ('34), Smith and Swingle ('38),

Swingle and Smith ('39 *et seq.*), and by fish hatchery workers in general. Such an established usage is unlikely to disappear, but whenever complete clarity is desired an unambiguous term should be substituted.

5. *Net increase or decrease.* The difference in weight of a fish population at the beginning and end of a period of time is its net increase (or decrease). This too, has been referred to as "production," for example by Morris and Hale ('42), who used the term for the increase in weight of a population of young bass over a period of about 2 months.

In much work with pondfishes the initial weight of fry stocked is so small as to be negligible in comparison with the final weight of the fingerlings at the end of the growing season, so that for practical purposes the net increase in such cases is equivalent to the standing crop at that time, which, if it is removed and used, also becomes the yield. It is possible that some of the authors cited in Section 4 have really thought of "production" in terms of net increase and ignored the initial weight of their stock only because it was so small.

6. *Recoverable weight.* Recently, many fish populations containing undesirable species have been killed with rotenone (Krumholz, '48). The weights of fishes recovered during such studies have been referred to as carrying capacities, standing crops, total population weights, estimates of fish production, etc. (Eschmeyer, '38; Thompson and Bennett, '39a, '39b, '39c; Thompson, '41; Smith, '41; Meehan, '42; Ricker, '42; O'Donnell, '43; and others). Even if the entire population were killed, there is no reason to believe that all of the fish are recovered. It has been pointed out by Krumholz ('44) and others that in such studies many things may contribute to the difficulty of retrieving all the fish; some may sink to the bottom and disintegrate there, and birds and mammals may visit the scene and eat some of fish before they can be recovered. In any event, the weight of only those fish that

were actually recovered during the study is known and for that figure the term *recoverable weight* is proposed.

Field observations indicate that difficulties, similar to those encountered in studies using rotenone, may occur when ponds are drained. If a pond is drained and the fish removed, the recoverable weight may closely approach the total weight of the population depending on the thoroughness of the search for fish that may have become stranded during the drawdown. If such a search is thorough, the recoverable weight is, for all practical purposes, the total weight. If no thorough search is made, or can be made, the recovered weight is not necessarily that of the entire population.

It is conceivable that, in a particular and hypothetical case, the carrying capacity, the recoverable weight, the standing crop, and even the yield may all be indicated by the same figure. In such an instance the body of water in question would necessarily be supporting as great a fish population as possible on a sustained basis, and the total weight of that population would have to be recovered and used.

DATA FROM MAXINKUCKEE PONDS

Recently it has come to our attention that fish populations in ponds stocked on an experimental basis undergo considerable variation in size and composition. Even though essentially the same kinds and numbers of fishes were placed in apparently similar ponds, there were marked differences in the populations at the end of each of 2 summers. In all ponds there were increases in the total weight of each population during each of the first 2 summers. Further, there was a noticeable decrease in the total weight of each population during the intervening winter.

Five ponds near Culver, Indiana, known as the Maxinkuckee Ponds, were used in the present experiment. Those ponds were built by the Maxinkuckee Rod and Gun Club over a period of years during the 1930's. All of the ponds referred to

here are underlain with marl and the levees are largely made up of that substance. The water is furnished by artesian wells, each pond having an individual well. There are separate outlets for each pond. In the shallower parts of all ponds cat-tails and rushes grow profusely whereas the deeper parts of the ponds support a growth of *Chara*. To all outward appearance the ponds are quite similar.

In May 1946, the 5 Maxinkuckee Ponds were stocked with adult fish of various species. Four of the ponds (Ponds 5, 6, 7, and 8) received largemouth black bass (*Micropterus salmoides*) and bluegills (*Lepomis macrochirus*). In addition, black crappies (*Pomoxis nigro-maculatus*) and bowfin (*Amia calva*) were placed in Ponds 5 and 7. Pond 9 was stocked with bluegills only. No fertilizer was added to any of the ponds. Water levels in all of the ponds were kept as constant as possible throughout the experiments. The fish were not fed at any time and they were left in the ponds to reproduce as they would. All of the ponds were drained in October 1946, May 1947, and October 1947. At each of those times samples of the individual lengths and weights of the various age groups of each species were taken and the total weight of each population obtained. The fish were then returned to the ponds from which they had been taken, the ponds having been refilled in the meantime. In some instances, other kinds of fishes, notably killifishes (*Fundulus diaphanus menona*) and mudminnows (*Umbra limi*), were captured when the ponds were drained. In such cases those fish were destroyed. Thus, a running account of any changes that occurred in the populations during the first summer, the subsequent winter, and the second summer was obtained. The total weight of the population in any pond was not the same any two times that the pond was drained, with the single exception of that in Pond 5. There, muskrats tunnelling in the levee during the winter of 1946-47 caused a leak to develop that so lowered the water

TABLE I. *Total weights of fish populations, in pounds per acre, in each of the five Maxinkuckee Ponds. The dates indicate when the ponds were drained*

| | Pond 5 | Pond 6 | Pond 7 | Pond 8 | Pond 9 |
|---|--------|--------|--------|--------|--------|
| May 1946 | 20.5 | 11.0 | 16.6 | 7.6 | 7.7 |
| October 1946 | 78.5 | 111.1 | 67.8 | 20.6 | 62.7 |
| May 1947 | 20.6 | 67.8 | 47.1 | 16.4 | 52.0 |
| October 1947 | 126.8 | 194.7 | 141.4 | 55.3 | 169.4 |
| Percentage decrease over winter | 73.8* | 39.0 | 29.0 | 20.4 | 17.0 |
| Percentage increase from Oct. 1946 to Oct. 1947 | 61.5 | 75.2 | 108.6 | 168.4 | 154.2 |

* This figure is distorted for reasons given in the text.

level as to expose much of the shallower pond floor. Such tunnelling occurred several times during the winter and, although the levee was repaired as soon as possible, it is presumed that some abnormal loss of fish occurred. As a result, the total weight of the population in May 1947 was very nearly that of May 1946. In every pond the total weight of the population increased during each summer, and the weight attained by the end of the

second summer was considerably greater than that reached during the first (table I, figure 1).

During the interval between the draining of the ponds in October 1946 and May 1947, there was a decrease in the total weight of the population in each of the 5 ponds (table I, figure 1). The over-winter loss ranged from 20.4 per cent to 39.0 per cent of the total population. The 73.8 per cent loss over winter in Pond 5,

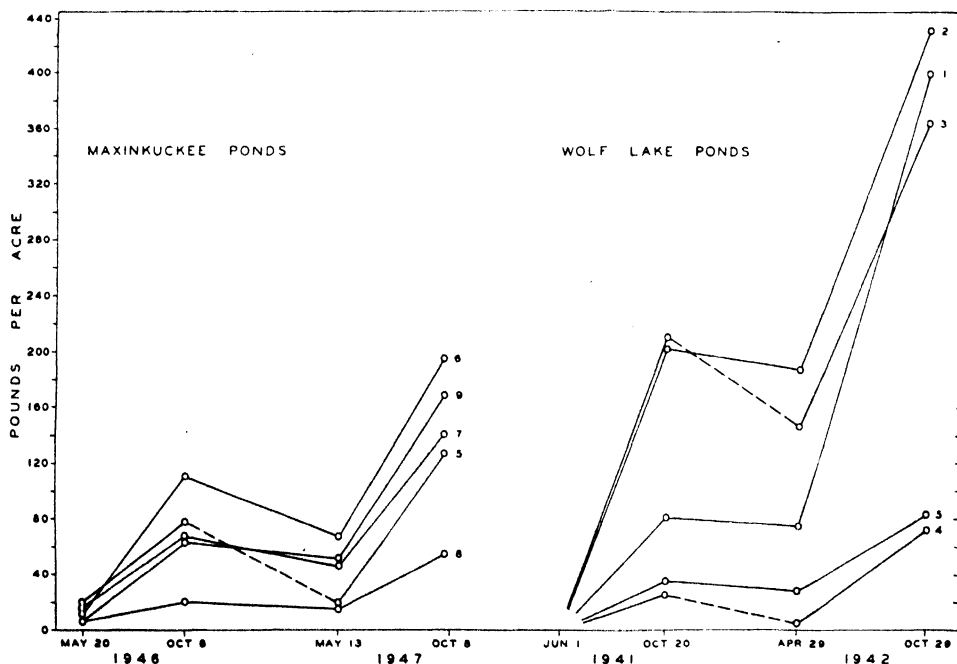


FIG. 1. Total weights of fish populations of five ponds at Wolf Lake Hatchery (right) and five ponds near Culver, Indiana (left) in pounds per acre. The broken lines in the curves indicate that there was considerable loss in weight during that period due to unnatural causes.

TABLE II. *Average lengths in millimeters and average weights in grams of bluegills of the 1946 year class taken from the Maxinkuckee Ponds, near Culver, Indiana, at the end of the first summer, the following winter, and the second summer. The figures in parentheses indicate the number of fish in the population*

| | Pond 5 | | Pond 6 | | Pond 7 | | Pond 8 | | Pond 9 | |
|--------------|-----------------|--------|------------------|--------|-----------------|--------|----------------|--------|------------------|--------|
| | Av. L. | Av. W. | Av. L. | Av. W. | Av. L. | Av. W. | Av. L. | Av. W. | Av. L. | Av. W. |
| October 1946 | 50.5 (7,954) | 2.9 | 48.4 (18,476) | 2.0 | 48.3 (7,193) | 2.8 | 56.6 (448) | 4.0 | 40.4 (15,307) | 1.3 |
| May 1947 | 61.0 (968) | 4.1 | 53.5 (7,255) | 2.9 | 52.9 (4,138) | 2.7 | 66.0 (364) | 5.4 | 44.6 (10,706) | 1.7 |
| October 1947 | 125.3 (791) | 42.3 | 84.7 (5,465) | 11.2 | 86.6 (2,926) | 13.7 | 125.9 (278) | 44.4 | 74.0 (8,492) | 7.4 |

which is considerably out of line with the others, is to be attributed to the lowering of the water level as mentioned earlier. Such decreases in the total weights of the populations are not traceable to weight losses in the individual fish of the dominant species inasmuch as the average lengths and weights of those fish in each population showed increases during that period, as indicated in tables II and III. Those tables show the average lengths and weights of the bluegills and bass of the 1946 year class respectively each time the ponds were drained. Not only were there over-winter increases in the average sizes of those species but there were also increases in their minimum and maximum lengths with the single exception of the maximum length of the bluegills in Pond 8. There the sample showed a decrease

of 2 millimeters. The data on the minimum, average, and maximum lengths of the bluegills and bass of the 1946 year class are graphically represented in figures 2 and 3 respectively. Here, the bases of the individual triangles indicate the size range of the fish under consideration each time the ponds were drained, whereas the peaks of the triangles represent the average lengths.

Any changes in weight experienced by the adult centrarchids were, in general, the same as those of the 1946 year class. Adult bass and bluegills showed increases in individual lengths and weights over winter in all ponds and any loss in total weight of those groups was attributable to loss in numbers.

Conversely, the two bowfins that were placed in Pond 5 weighed approximately 1800 grams in June 1946. By the end of the summer their combined weight had increased to 2630 grams. During the ensuing winter that weight fell to 2370 grams and then rose to 3650 grams by the end of the second summer. The same situation held for the single bowfin in Pond 7. Here, the over-winter loss in weight was traceable to a direct loss in weight in the individual fish as there was no decrease in numbers. In addition to the over-winter loss in weight in individual bowfins, there was a concurrent loss in average length of 10 millimeters in each of the three individuals.

The species compositions of the popula-

TABLE III. *Average lengths in millimeters and average weights in grams of largemouth black bass of the 1946 year class taken from the Maxinkuckee Ponds, near Culver, Indiana, at the end of the first summer, the following winter, and the second summer. The figures in parentheses indicate the number of fish in the population*

| | Pond 5 | | Pond 8 | |
|--------------|---------------|--------|----------------|--------|
| | Av. L. | Av. W. | Av. L. | Av. W. |
| October 1946 | 80.6 (416) | 7.7 | 72.7 (483) | 6.2 |
| May 1947 | 90.9 (86) | 10.3 | 77.7 (340) | 6.0 |
| October 1947 | 199.0 (74) | 114.7 | 142.7 (164) | 38.9 |

tions in the Maxinkuckee ponds in which more than one kind of fish was present changed considerably during the first two summers and the intervening winter.

The percentages of the total weight of the population contributed by the different species each time the ponds were drained are shown in table IV. The data indicate

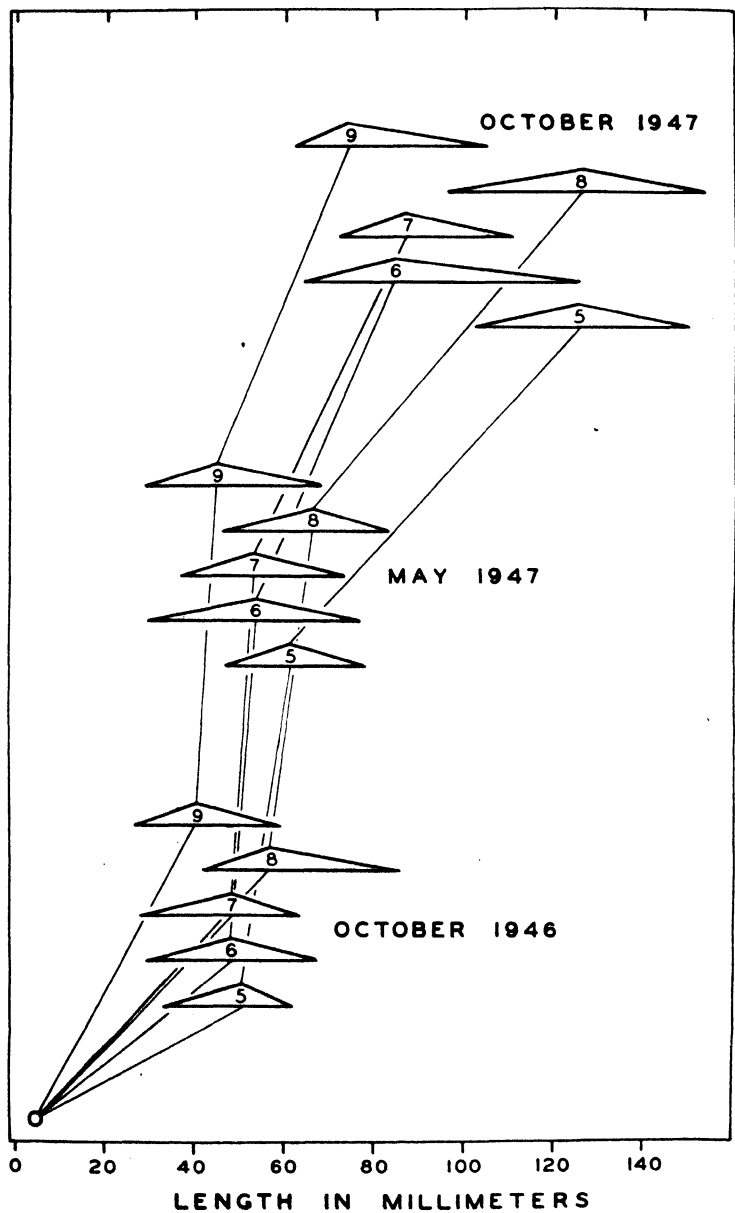


FIG. 2. Size ranges and average lengths of bluegills of the 1946 year class from 5 Maxinkuckee Ponds at the different times they were drained. The bases of the individual triangles indicate the size ranges whereas the peaks indicate the average lengths. The numbers in the triangles indicate the pond population to which the data refer.

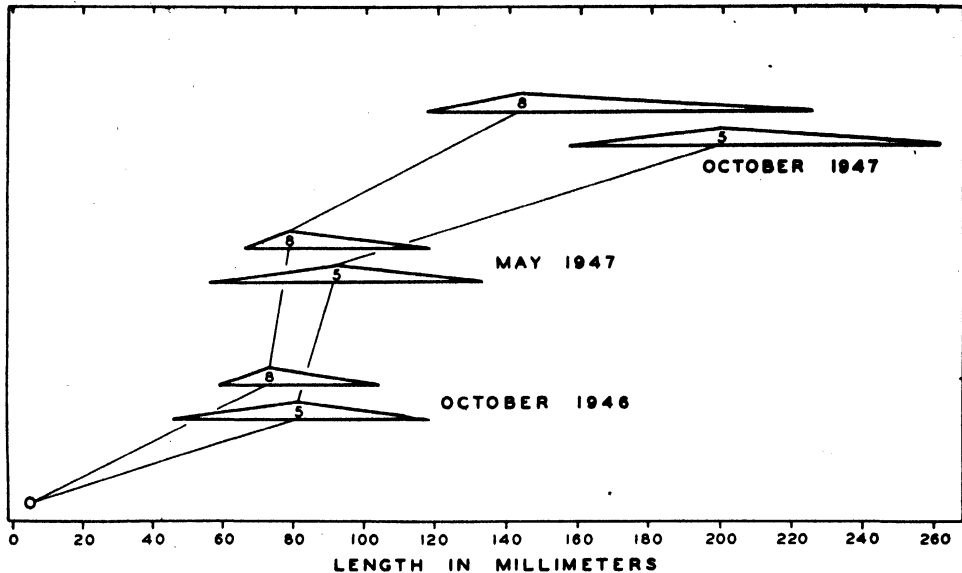


FIG. 3. Size ranges and average lengths of largemouth bass of the 1946 year class from 2 Maxinkuckee ponds at the different times they were drained. The bases of the individual triangles indicate the size ranges whereas the peaks indicate the average lengths. The numbers in the triangles indicate the pond population to which the data refer.

that bluegills, which are more prolific than largemouth bass, tend to get the

TABLE IV. Percentage of total weight of fish population in each of four ponds near Culver, Indiana, contributed by each species in the population. The "other fish" listed in the column on the extreme right were largely top minnows and/or mud minnows

| | Blue-gills | Large-mouth bass | Black crappies | Bow-fin | Other fish |
|---------------|------------|------------------|----------------|---------|------------|
| <i>Pond 5</i> | | | | | |
| May 1946 | 36.2 | 31.9 | 11.7 | 20.2 | — |
| October 1946 | 69.0 | 20.7 | 2.2 | 7.1 | 1.0 |
| May 1947 | 52.9 | 15.2 | 5.4 | 26.4 | 0.1 |
| October 1947 | 74.2 | 17.4 | 1.7 | 6.7 | — |
| <i>Pond 6</i> | | | | | |
| May 1946 | 38.8 | 61.2 | — | — | — |
| October 1946 | 88.1 | 10.4 | — | — | 1.5 |
| May 1947 | 81.4 | 17.5 | — | — | 1.1 |
| October 1947 | 81.3 | 18.7 | — | — | — |
| <i>Pond 7</i> | | | | | |
| May 1946 | 48.4 | 23.4 | 15.2 | 13.0 | — |
| October 1946 | 79.1 | 11.8 | 4.7 | 4.4 | — |
| May 1947 | 72.7 | 17.6 | 3.7 | 6.0 | — |
| October 1947 | 73.8 | 22.9 | 0.6 | 2.7 | — |
| <i>Pond 8</i> | | | | | |
| May 1946 | 52.1 | 47.9 | — | — | — |
| October 1946 | 34.5 | 58.2 | — | — | 7.3 |
| May 1947 | 43.6 | 55.5 | — | — | 0.9 |
| October 1947 | 52.4 | 47.3 | — | — | 0.3 |

jump on the bass and maintain it. In only one instance out of the 4 ponds did the bass outweigh the bluegills at the end of the first summer (Pond 8). Even then the bass were unable to hold their own and by the end of the second summer the bluegills had overtaken them. Further, it is apparent that black crappies, as stocked in this experiment, were unable to compete successfully against largemouth bass and bluegills for a position of importance in a pond. In Ponds 5 and 7, where black crappies were stocked along with bass and bluegills, the crappies did not reproduce very successfully in either pond and by the end of the second summer had very nearly been crowded out of both ponds.

It should be mentioned here that the bluegills reproduced successfully in all ponds during each of the 2 summers. The bass, on the other hand, reproduced successfully only in Ponds 5 and 8 during the first summer and in only Ponds 6, 7, and 8 during the second summer. The crappies did not reproduce to any great extent in any pond either year. There was no reproduction by the bowfin.

TABLE V. *Total weights of fish populations, in pounds per acre, in each of five ponds at the Wolf Lake Hatchery, near Kalamazoo, Michigan.* The dates indicate when the pond was drained. The ponds were stocked in July 1941 with bluegill fry that were not weighed. Tr indicates trace, the weights of the fry being negligible

| | Pond 1 | Pond 2 | Pond 3 | Pond 4 | Pond 5 |
|---|--------|--------|--------|--------|--------|
| June 1941 | Tr | Tr | Tr | Tr | Tr |
| October 1941 | 81.6 | 203.2 | 211.7* | 26.3** | 35.7 |
| April 1942 | 74.9 | 187.9 | 146.6 | 4.9 | 28.1 |
| October 1942 | 399.6 | 431.1 | 364.2 | 72.3 | 83.1 |
| Percentage decrease over winter | 8.2 | 7.5 | 4.9 | 42.0 | 21.3 |
| Percentage increase from Oct. 1941 to Oct. 1942 | 389.7 | 112.2 | 72.0 | 174.9 | 132.8 |

* Of these, 57.5 pounds per acre of green sunfish that had entered the pond during the summer were destroyed when the pond was drained in October 1941.

** Of these, 17.5 pounds per acre of Iowa darters (*Poeciliichthys exilis*) that had entered the pond during the summer were destroyed when the pond was drained in October 1941.

DATA FROM WOLF LAKE HATCHERY PONDS

In general, the findings on changes in the total weights of the fish populations at the Maxinkuckee Ponds are corroborated by unpublished data on bluegill populations obtained by the writer while employed at Michigan's Institute for Fisheries Research.* In June 1941, 5 ponds at the Wolf Lake Hatchery, near Kalamazoo, Michigan, were stocked with bluegills at the "golden fry" stage (yolk fry) at different intensities in an attempt to obtain information on differences in growth rate as influenced by the various rates of stocking. One of the ponds

(Pond 1) was fertilized with 100 pounds of Swift and Company's 10-6-4 (N-P-K) commercial fertilizer along with 25 pounds of lime once a month for 4 months each summer. Other than that no attempt was made to alter the fertility of the ponds. Measurements of size and weight of the fish were made similarly as in the present experiment, i.e., at the end of the first summer, at the end of the ensuing winter, and at the end of the second summer. Here, as in the Maxinkuckee Ponds, the total weight of each population increased during the first summer, fell off during the winter, and then increased during the second summer to a much greater weight than that achieved during the first summer (table V, figure 1). The great over-winter loss in Pond 3 is to be attributed to the removal of 57.5 pounds of

* The writer is grateful to Dr. A. S. Hazzard, Director of the Institute for Fisheries Research of the Michigan Department of Conservation, for permission to use these data.

TABLE VI. *Average lengths in millimeters and average weights in grams of bluegills of the 1941 year class taken from ponds at the Wolf Lake Hatchery, near Kalamazoo, Michigan, at the end of the first summer, the following winter, and the second summer.* The figures in parentheses indicate the number of fish in the population

| | Pond 5 | | Pond 6 | | Pond 7 | | Pond 8 | | Pond 9 | |
|--------------|-------------------|--------|------------------|--------|------------------|--------|----------------|--------|------------------|--------|
| | Av. L. | Av. W. | Av. L. | Av. W. | Av. L. | Av. W. | Av. L. | Av. W. | Av. L. | Av. W. |
| October 1941 | 26.2 (114,393) | 0.3 | 44.7 (92,900) | 1.6 | 51.8 (32,349) | 1.9 | 79.7 (423) | 9.6 | 100.3 (1,133) | 17.6 |
| April 1942 | 29.7 (80,499) | 0.4 | 50.8 (63,898) | 2.1 | 52.6 (18,888) | 2.6 | 86.1 (204) | 10.9 | 100.6 (804) | 17.9 |
| October 1943 | 58.9 (54,450) | 3.0 | 80.8 (40,273) | 7.7 | 99.8 (3,951) | 14.6 | 144.8 (183) | 46.9 | 151.9 (618) | 65.0 |

green sunfish (*Lepomis cyanellus*) per acre, in October 1941, which had presumably entered the pond as fry from the pond above it. The water system at the Wolf Lake Hatchery is so arranged that the overflow from one pond oftentimes goes directly into another pond. The

over-winter decrease in Pond 4 is attributable to the removal of 3543 Iowa darters (*Poeciliichthys exilis*), amounting to 17.5 pounds per acre, in October 1941. Here, again, these fish had probably entered through the water system.

Just as in the Maxinkuckee Ponds, the

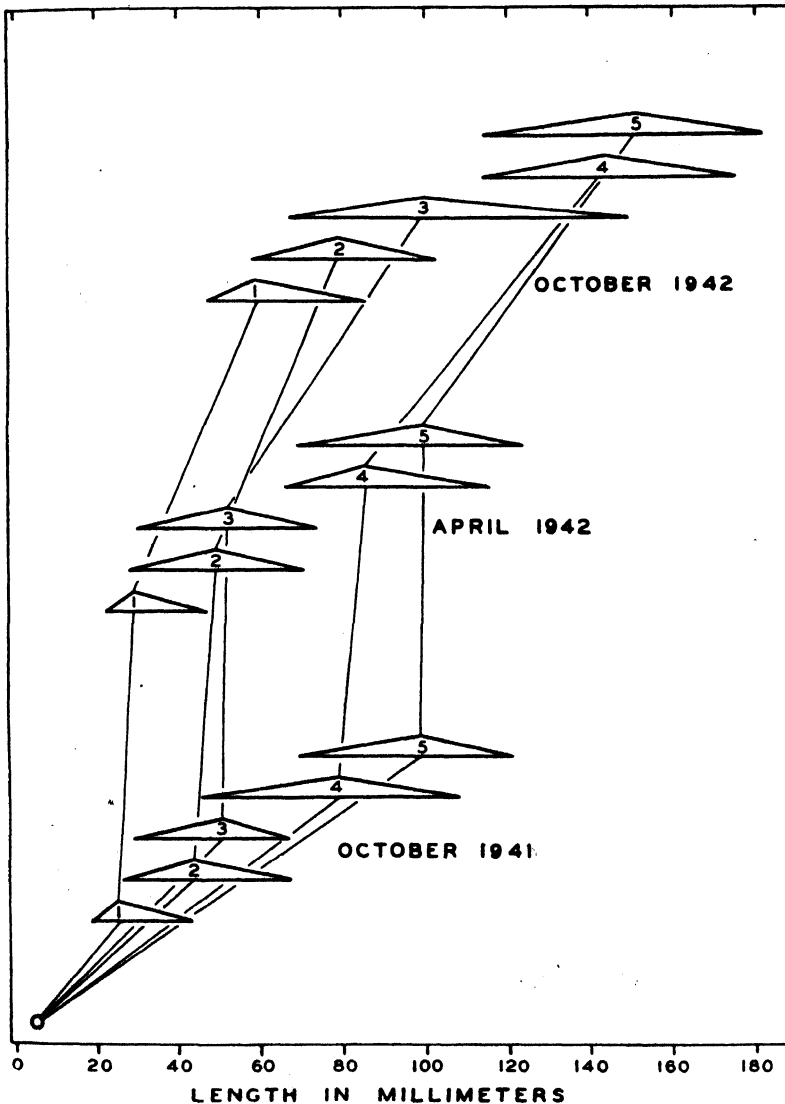


FIG. 4. Size ranges and average lengths of bluegills of the 1941 year class from 5 ponds at the Wolf Lake Hatchery at different times they were drained. The bases of the individual triangles indicate the size ranges whereas the peaks indicate the average lengths. The numbers in the triangles indicate the pond population to which the data refer.

over-winter losses in weight in the bluegill populations in the ponds at the Wolf Lake Hatchery are not traceable to losses in the individual fish but rather to losses in numbers. The average lengths and weights of the bluegills from each of the 5 ponds at the Wolf Lake Hatchery each time they were drained are shown in table VI; the minimum, average, and maximum lengths of the bluegills in each pond are illustrated in figure 4.

Unfortunately, the experiments at the Wolf Lake Hatchery were terminated at the end of the second summer.

DISCUSSION

It is obvious from the experimental data that there are considerable differences in the total weights of fish in different ponds at any one time regardless of the species composition of the population. As mentioned earlier, the fertility of a pond is thought to be closely linked with the fertility of the soil in which it stands. At the Wolf Lake Hatchery, Ponds 1 and 2 were muck-bottomed, Ponds 4 and 5 were sand-bottomed, and Pond 3 was part sand and part muck. The total weights of the fish in Ponds 1 and 2 were considerably greater than those in Ponds 4 and 5 and that of Pond 3 was intermediate. However, in the Maxinkuckee Ponds, all ponds were built in the same kind of soil and to all outward appearances were very similar. Still, the total weights of fish in those ponds ranged from 20.6 (Pond 8) to 111.1 (Pond 6) pounds per acre at the end of the first summer and by the end of the second summer those weights had increased to 55.3 and 194.7 pounds per acre respectively. The causes for such wide ranges in total weight are not readily obvious. Certainly they do not seem to be attributable to differences in the natural fertility of the ponds themselves. Further, the differences are not traceable to species composition of the population inasmuch as both Ponds 8 and 6 contained largemouth bass and bluegills.

Also, from the experimental data, there is evidence that populations consisting of bluegills alone increase at a more rapid rate than those in which piscivorous fish are present in reasonably large numbers. In all populations that were made up of bluegills only, whether at the Wolf Lake Hatchery (Ponds 1, 2, 4, and 5, table V) or the Maxinkuckee Ponds (Pond 9, table I), the total weights of the populations increased an average of 192.8 per cent from the end of the first summer to the end of the second. In all other ponds there were some kinds of piscivorous fish present; in the Maxinkuckee Ponds such fish were largemouth bass, black crappies, and bowfin, whereas in Pond 3 at the Wolf Lake Hatchery very nearly one-fourth of the total population of October 1941 consisted of green sunfish. In those ponds the increase in total weight of the population from October to October was 91.7 per cent or only about half of that which occurred in the pure bluegill populations. At first glance one might think that the presence of the predators checked the bluegills so that the rate of increase was slowed down. However, in the Maxinkuckee Ponds, the bluegills kept increasing in all ponds in spite of the presence of the bass. Further, even though the total weights of the populations containing both bluegills and bass increased during each of the two summers, the bluegills increased at a considerably greater rate than the bass and therefore made up a greater percentage of the total weight of the population at the end of the second summer than at the end of the first in all cases. One of the reasons why the weight of bluegills increased at a greater rate than that of the bass is that the bluegills, as mentioned previously, reproduced successfully each year in all of the Maxinkuckee Ponds whereas the bass enjoyed successful reproduction only in 2 ponds during the first year (1946) and in 3 during the second. In only one pond (Pond 8) did the bass reproduce successfully during both years and it was only in that pond that they even approached

keeping the bluegills in check. Thus it seems that largemouth bass, although predatory in nature, are not necessarily capable of keeping bluegills in check.

In October 1941, when Pond 3 at the Wolf Lake Hatchery was drained, there was an estimated total of 3184 green sunfish present. Of those, 362 of the largest ones were destroyed, leaving a total of 2822. The following April, 2044 green sunfish were present, a survival of 74.2 per cent over winter as compared with a 59.9 per cent survival of bluegills of the same age group in the same pond. Of the 2044 green sunfish taken in April, 1635 were destroyed leaving a remainder of 409 (19.1 pounds per acre). Some of those fish were seen spawning during the summer of 1942 whereas the bluegills, although of the same age, were not sufficiently mature. When the pond was drained in October 1942, there was an estimated total of 48,500 green sunfish that weighed 187.2 pounds per acre, very nearly a ten-fold increase during the summer. It may be that all of those green sunfish were not spawned in Pond 3 inasmuch as some may have entered as fry as in 1941. During the same period the bluegills, which numbered 31,686 individuals (154.2 pounds per acre) in October 1941, dropped off to a mere 3905 individuals (145.9 pounds per acre) in October 1942. From the foregoing account it is apparent that green sunfish are capable of overtaking bluegills in a pond in which they were originally outnumbered and quickly becoming the dominant fish.

It has been mentioned by Thompson ('41), Bennett ('43, '44), and others that there is considerable variation in the weight of individual species in a fish population. Apparently such fluctuations do not come and go rapidly but rather extend over a period of years. One species usually increases at the expense of another and, although the total weight of the population may remain more or less constant, there are oscillations in the weights of the

various species comprising that population.

Although the total weights of the populations in the Maxinkuckee Ponds may yield information on the carrying capacities of those ponds at a later date there is no reason to believe that those capacities were reached during either of the first 2 summers. No attempt was made to alter the fertility of those ponds during 1946 or 1947 and yet the weights of the populations very nearly doubled between the end of one summer and the next. Certainly it is obvious that the carrying capacity had not been reached in any of the ponds by the end of the first summer.

Swingle and Smith ('41:221) stated that a fish population, whatever the stocking method, reaches its maximum weight of fish per acre within 12 to 15 months, and after that there is little or no increase in the total weight unless there is a radical shift in the dominant species. Thompson ('41:209) indicated that the fish population of Lake Senachwine adjusted itself to tremendous fluctuations in the area of the lake within a single growing season, the total weight per acre remaining about constant. However, as in the Maxinkuckee Ponds, it seems unreasonable that a population that has doubled its weight during the second summer of its existence should suddenly have reached its maximum by the end of that summer and levelled off. A continuation of the experiments at the Maxinkuckee ponds will shed light on this question.

SUMMARY

The total weights of fish populations in 10 ponds, stocked on an experimental basis, increased during each of 2 summers. The weight attained at the end of the second summer was considerably greater in all cases than that reached during the first summer.

During the intervening winter the total weights of the populations decreased in all ponds. Such losses were traceable to losses in numbers of fishes among centrar-

chids inasmuch as the individuals increased in both length and weight. Individual bowfin experienced losses in both length and weight during that period.

There were considerable differences in the total weights of fish in apparently similar marl-bottomed ponds that had been similarly stocked. Those differences were manifest at the end of the first summer, the ensuing winter, and the second summer.

Largemouth black bass, although predatory on other fishes by nature, were unable to keep bluegill populations in check. The bass, which spawned successfully in only 2 of 4 ponds the first summer and in 3 of 4 the second year, were consistently outweighed by the bluegills, which spawned successfully in every pond each year.

Green sunfish, although greatly outnumbered by bluegills of the same age group at the beginning of the first summer, overtook the bluegills and completely outnumbered and outweighed them by the end of the second summer.

Black crappies were unable to compete successfully against largemouth bass and bluegills in the 2 ponds in which they were stocked.

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PLANT COMMUNITIES IN THE VICINITY OF THE VOLCANO EL PARÍCUTIN, MEXICO, AFTER TWO AND A HALF YEARS OF ERUPTION¹

WILLIS A. EGGLEER

Department of Biology, Newcomb College, Tulane University, New Orleans

INTRODUCTION

Volcanoes exert a great influence upon plant communities contiguous to them. While active they destroy the member plants. Their ejecta may so alter soil conditions that processes of plant succession requiring centuries to complete may be set in motion. There is now little specific information on these subjects. Krakatao has long been considered a classic example, but there is now some doubt if it is as valuable as presumed. Backer ('29) states that many false assumptions were made by the early workers and that actually little is known about the biological aspects of Krakatao. Katmai Volcano, Alaska, was studied from the time of its eruption and some phases of its revegetation have been reported by Smith and Griggs ('32), and Griggs ('33). Gadow ('30) reported his observations of the volcano Jorullo, Mexico (see fig. 1), and also summarized the literature. Lawrence ('39, '41) has studied the problem on Mount St. Helens, Washington. The present author has contributed to the subject in a study of extinct volcanoes in Craters of the Moon National Monument, Idaho (Eggler '41).

An opportunity to learn new details about the effects of volcanoes on vegetation presented itself when the Parícutin Volcano in the state of Michóacán, Mexico, began eruption on February 20, 1943. Two and a half years later the author and his assistant, Robert Hakala, visited the volcano for a three-month period, July through September, 1945. The work had three main objectives: 1. To learn the character of the plant communities about

the volcano before the eruption began. 2. To find what effect volcanism had had upon the environment and upon vegetation, and, to learn how the vegetation was reacting under the changed conditions. 3. To lay groundwork for later studies of the process of revegetation. I hope to revisit the area at intervals over an extended period to add to the information presented in this paper.

DESCRIPTION OF THE REGION

Geography

Parícutin Volcano lies among masses of rugged volcanic mountains which form part of the southern end of the Central Mexican plateau (see fig. 1). Immediately to the south is the large Cerro (Mount) Tancítaro whose summit rises to nearly 13,000 feet (fig. 3). To the northeast is a smaller mountain mass, formed of several volcanoes, the nearest being Cerro Angáhuán (10,594 feet high),² which are much younger than Tancítaro. Hundreds of smaller volcanic cones, many about the size of Parícutin, lie about in all directions. Most of the plateau land between the cones varies from 7,000 to 7,800 feet in elevation.

The studies reported here were made in an area roughly rectangular, with Parícutin located about at the center. It lies east and north of the summit of Tancítaro which occupies one corner (fig. 2).

Geology

Williams ('45) has discussed the geologic setting of Parícutin rather fully. The

¹ This work was accomplished through the support of a grant from the American Philosophical Society. I am truly grateful for the aid.

² Altitudes given in this paper are unofficial and not verified. No others were available. Altitude at the summit of Cerro Angáhuán was determined by the present author with an aneroid barometer. The value for Tancítaro is that accepted by local residents but it is not verified.

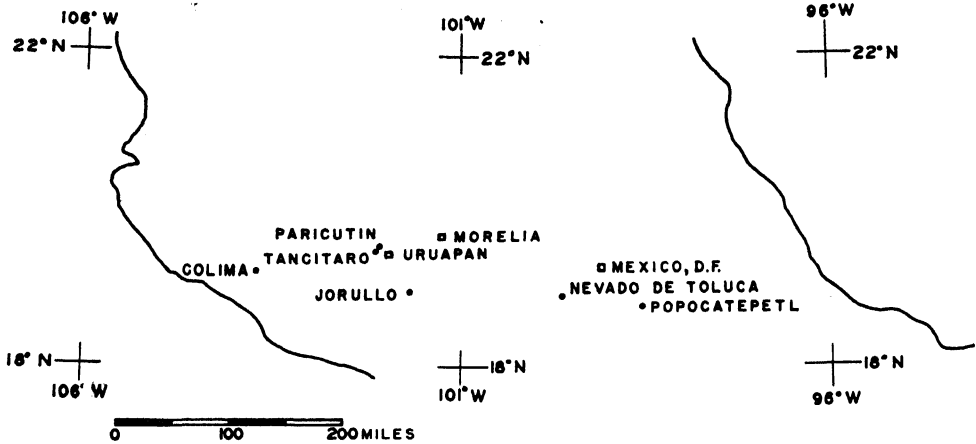


FIG. 1. Map of Central Mexico, showing location of Paricutin, some large volcanoes (dots), and important cities (squares).

eruption of Paricutin is the most recent incident in a long history of volcanism which extends back to Tertiary time. A wide belt of volcanoes, more than 500 miles

long, crosses Mexico, approximately along the nineteenth parallel. In this belt are such giants as Popocatépetl, Nevado de Toluca, and Colima, as well as myriads of

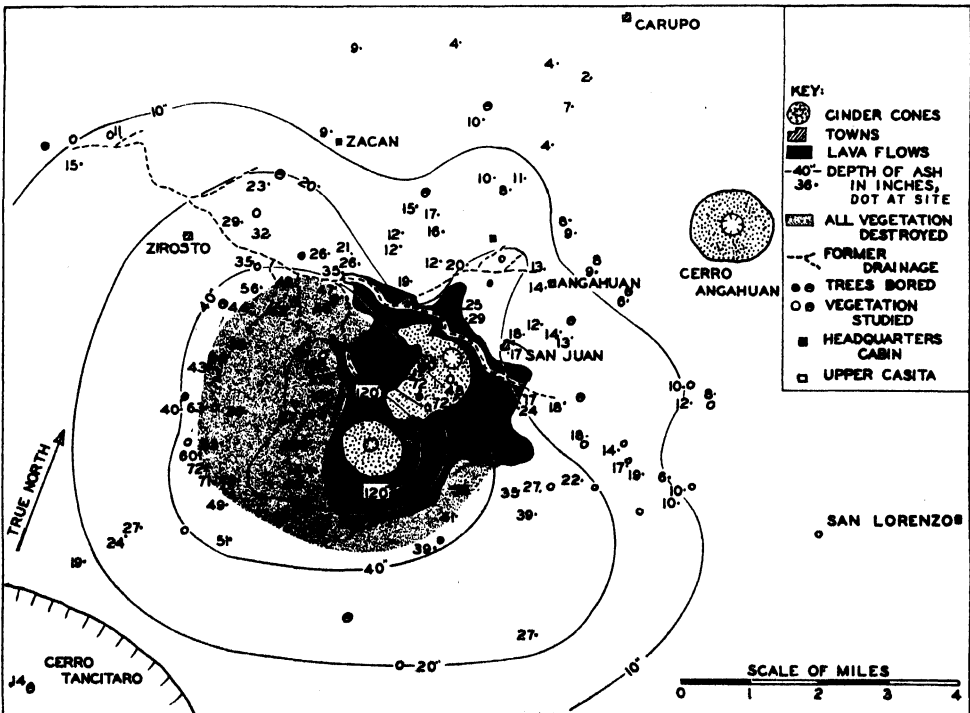


FIG. 2. Map of the study area, showing locations of villages, positions of cinder cones, extent of lava flows, depths of ash at the points where measured, sites where vegetation was studied, and extent of vegetation destruction as of September, 1945. Paricutin Volcano is the southernmost cinder cone.

smaller ones, most without published names. The two youngest are Jorullo, which began eruption in 1759, and Parícutin. These are about 50 miles apart (fig. 1).

Probably no single small, geologic incident has been honored with more writings that has Parícutin during the early years

('44), Segerstrom and Gutierrez ('47), and Wilcox ('47, '47a).

In the summer of 1945 the central figure of Parícutin was a symmetrical cinder cone whose summit stood about 1,500 feet above the field on which it began to deposit, and whose base was a mile across (fig. 3). A field of aa³ lava, about five



FIG. 3. Parícutin Volcano in eruption. Highest mass in background is Cerro Tancítaro. Village is Angáhuán. Photo from Cerro Angáhuán. August, 1945.

FIG. 4. Corn plants 7 to 8 feet tall growing in village of Angáhuán. August, 1945.

of its life. The most complete history is that by Ordoñez ('45), in which he relates the events from the beginning of activity to the end of December, 1944. Shorter periods, ranging from two days to fourteen weeks have been reported by others. A partial list includes Egger ('45), Kennedy ('46), Krauskopf ('46, '46a), Krauskopf and Williams ('46), Lawrence

square miles in extent and varying from about fifty to a few hundreds of feet in thickness, had flowed from several vents near the base of the cinder cone. Extending for several miles in all directions from the main orifice was a mantle of ash (fig.

³ Aa lava breaks into fragments as it moves and cools. Surfaces of these flows are jagged and broken.

2). All material which Parícutin has ejected is basaltic in character, and when unweathered is nearly black in color (figs. 6, 7, 8). Gratan ('45) has pointed out that Parícutin is a typical example of the volcanoes of the region. It is likely its history will be a repetition of that of the hundreds of its older fellows.

Soil

Soil derived from volcanic ash is usually fertile and all soil in this area was directly or indirectly of that origin. Where exposed through the new volcanic deposits it is generally fine in texture and very deep. A chief limitation to agriculture has been the scarcity of land level enough to cultivate. Occasionally one sees attempts to grow crops on the slopes of old volcanoes, but the erosion which results when such land is cleared and the soil cultivated indicates that it would be better left in native vegetation. No terracing is done in this particular part of Mexico.

Climate

The climate of the region is distinctly temperate in character, without frost at the altitude of the study area. Cool temperatures prevail throughout the year. A dry season, from November through May, is followed by a rainy, humid, summer and autumn. Temperature and precipitation records for a period of 15 years are available for the cities of Uruapan and Morelia (fig. 1).⁴ Uruapan is 12 miles southeast, at an altitude of 5,285 feet, compared with about 7,400 at the volcano. In Uruapan January is the coldest month, with a mean of 61 degrees F. May is the warmest month, with a mean of 72.3 degrees. During the years of the record the maximum temperature recorded was 97.7 degrees, and the minimum 41. Average annual rainfall is 66.2 inches. September has the highest monthly rainfall, with 16 inches, and April the lowest, with 0.16. Morelia

is about 80 miles east of the volcano at 6,309 feet elevation. Its temperatures generally run lower than those in Uruapan. May has a mean of 68.9 degrees, January a mean of 57. The maximum recorded during the 15 years is 87.9 degrees, and the minimum is 34.9. Average annual precipitation is 30.7 inches. July is high with 6.7 inches, and December is low with 0.2. Temperatures near the volcano are probably similar to those of Morelia while precipitation is apt to be not greatly different from that of Uruapan.

Contreras Arias ('42) has prepared a climatological map of Mexico, based upon the system of Thornthwaite, in which two factors, temperature and precipitation, are considered of prime importance in determining the distribution of vegetation. The area of this study is described on the map as moderate in temperature, without a well defined winter cold season, dry, with especially dry winters.

Rains are usually of the flash type. Topography is rough near the volcano, hence effectiveness of precipitation is less than the total rainfall might suggest, because of the large amount lost in runoff.

Some observers believe volcanic activity has caused precipitation to increase, locally. Pough ('48) states that vapor emitted from the volcano may condense and fall as rain. Munns ('48) has a somewhat different theory. He suggests that convectional currents, resulting from the sustained heat of the volcano, bear aloft great masses of air. As these masses cool clouds form and rain results.

If it be true that rainfall has increased then erosion has also been increased. Other factors have also tended to increase erosion near the volcano. The subject is discussed at more length in another section of this paper.

Population and industry

Residents of the region are almost all Tarascan Indians who generally live in villages. In the area studied there had been seven villages, indicating their closeness and the density of population (figs. 2, 3). Two, San Juan Parangáricutiro

⁴ Climatic data were obtained from the Mexico City office of the Servicio Meteorológico Mexicano. The data were converted from metric and centigrade units to English and fahrenheit units by the present author.

(generally called San Juan), with a population of about 3,000 persons, and Paricutin, with about 800, had to be evacuated and were later destroyed by the volcano. The other villages all have populations of between 800 and 1,000 persons. Three of the five have suffered materially, Zacán and Zirósto most. In these two villages some buildings collapsed under the weight of ash, and nearly all the fields have been made useless. Angáhuan (figs. 3, 4) has had as much or more ashfall but it has been kept in a better state of repair. It too has lost the use of its fields in most instances, partly because of ash deposits and partly because of lava flows covering them. Carúpo village has been little affected by the volcano but some of its fields have been abandoned. San Lorenzo has been little influenced by the volcano. Fortunately there has been no loss of human life directly attributable to the volcano.

Agriculture has been the chief means of livelihood for the people. A family often worked several fields which may have been two or three miles apart. Maize is the main crop and yields are low, judging by the fields seen. After agriculture, turpentine was the chief source of income. Pine trees were tapped throughout the region at the lower altitudes about the site of the volcano. This industry has now been brought to a standstill by the volcano. Where trees were not killed the constant fall of ash into the collecting cups spoiled the sap. With loss of their fields and the turpentine industry many people have turned to the cutting of dead and dying timber for railroad ties and for sawlogs. It appears that they have been cutting too much living timber, along with the dead, for the future good of the forests and for stability of the human communities in general.

PLANT COMMUNITIES BEFORE VOLCANISM BEGAN

Prior to the eruption of Paricutin volcano about 75 per cent of the land of the region was forested (estimated from an aerial photo taken prior to February,

1943). This was generally the part too rough for agriculture. Conifers usually predominate in the forests, but hardwoods are also present, except at the highest altitudes.

There are three rather distinct vegetational zones. Occupying the plateau area between cones, and the sides of cones up to about 9,000 feet is a pine-oak forest. From 9,000 to about 10,000 feet fir is the dominant tree; and above 10,000 feet pines are dominant, continuing to the summit of even the highest mountain, Tancitaro. There is no timber line and trees do not appear to decrease in size with increased altitude.⁵

Pine-oak forest

This is the most important plant community from an economic standpoint as it covers the greatest area and furnishes forest products for local industry. It is variable in composition, ranging from mixed pine and hardwoods to nearly pure stands of pine or to almost pure hardwoods. Several sources of information were used in studying this community: general observations throughout the area, data on density and frequency from a mixed forest, and the ages and rates of growth of pine trees as obtained from increment cores.

General observations.—The most striking thing about this forest of lower altitudes, when first seen, is the predominance of pines over other tree species, particularly in the more level places. Two species, *Pinus leiophylla* Schl. & Cham.⁶

⁵ On higher mountains there may be distinct timber lines. On Popocatepetl, for example, which the writer visited, timber line begins very abruptly at around 12,000 feet. Here also pine is the timber-line tree. There was no indication of krumholz and trees appeared erect and healthy.

⁶ I am indebted to Dr. Paul Standley and Dr. J. A. Steyermark of the Chicago Museum of Natural History for the identification of most of the plant species. Many of the specimens collected were unavoidably poor because of the effects of volcanism. As a consequence positive identifications, particularly of the oaks which require the presence of good leaves, buds, and fruits, were often not possible.

and *P. pseudostrubus* Lindl., are about equal in importance and make up most of the pine population. A third, *P. teocote* Schl. & Cham., is of minor importance. When out-of-the-way spots, such as steep sides of cones some distance from a village or road, are examined it becomes evident that hardwoods, particularly oaks, are present and important. In many places they equal or exceed the pines in numbers. Continued observance reveals that even in areas where pines are dominant a few small hardwoods may be scattered among them and occasionally a large oak of great age is present. Eight oaks were identified from the area. These are *Quercus Fournieri* Trel., *Q. magnoliaefolia* Neé, *Q. mexicana* var. *angustifolia* H. & B., *Q. obtusata* H. & B., *Q. oligodontophylla* Trel., *Q. orbiculata* Trel. *Q. Radlkoferiana* Trel., and *Q. transmontana* Trel.

Next in importance among the trees, after *Pinus* and *Quercus*, are alder (*Alnus jorullensis* HBK.) and madroña (*Arbutus xalapensis* HBK.). In protected ravines are basswood (*Tilia Houghi* Rose), and fir (*Abies religiosa* (HBK.) Schl. & Cham.), in very small numbers. A cherry (*Prunus Capuli* Cav.), hawthorn (*Crataegus pubescens* (HBK.) Steud.), and ash (*Fraxinus Uhdei* (Wenzig) Lingelsheim),

are minor members of the community. They are more often along the margins of fields and in fence rows where they may have been planted.

Shrubs of importance in the pine-oak community are *Arctostaphylos rupestris* Rob. & Seat., *Ceanothus coeruleus* Lag., *Cestrum terminale* var. *latifolium* Francey, *Baccharis pteronoides* DC., *Buddleia parviflora* HBK., *Fuchsia Pringlei* Rob. & Seat., *Salix Hartwegii* Benth., and *Symphoricarpos microphyllus* HBK.

Statistical studies.—Forest in which *Quercus* is of major importance is relatively scarce and is generally confined to slopes of cones. This type of forest is dense, particularly in the shrub stratum. The south side of an old volcanic cone about 1,500 feet high and a mile in diameter at the base was chosen for detailed studies of this forest type. There were no evidence differences in the vegetation on different sides of this cone. The cone lay about two miles east of the village of San Lorenzo and ten from the volcano. It had been little affected by volcanism, beyond receiving a thin layer of ash on its surface, and seemed to be little disturbed by cutting and grazing. The angle of the slope was about 38 degrees where the study was made. Fourteen plots, 10 by 10 meters in size, were evenly spaced

TABLE I. Density and frequency of tree species in plots on south side of cone near San Lorenzo. Angle of slope about 38 degrees. Area, 1,400 square meters

| | Diameter size classes in inches | | | | | | | | |
|-------------------------------|---------------------------------|-----|-----|----|-----|----|------------|----|--------|
| | Less than 1* | | 1-3 | | 4-9 | | 10 or more | | Totals |
| | D. | F. | D. | F. | D. | F. | D. | F. | D. |
| <i>Symplocos prionophylla</i> | 2060 | 50% | 1 | 7% | 0 | 0% | 0 | 0% | 2061 |
| <i>Quercus magnoliaefolia</i> | 630 | 36 | 23 | 50 | 20 | 57 | 9 | 43 | 682 |
| <i>Taonabo Pringlei</i> | 280 | 43 | 11 | 29 | 7 | 14 | 1 | 7 | 299 |
| <i>Arbutus xalapensis</i> | 140 | 43 | 6 | 29 | 2 | 7 | 0 | 0 | 148 |
| <i>Quercus orbiculata</i> | 120 | 21 | 17 | 14 | 3 | 7 | 2 | 7 | 142 |
| <i>Pinus pseudostrubus</i> | 130 | 29 | 3 | 21 | 2 | 14 | 6 | 43 | 141 |
| <i>Pinus leiophylla</i> | 80 | 14 | 0 | 0 | 0 | 0 | 1 | 7 | 81 |
| <i>Alnus jorullensis</i> | 60 | 7 | 5 | 21 | 2 | 14 | 0 | 0 | 67 |
| <i>Quercus obtusata</i> | 0 | 0 | 20 | 14 | 7 | 14 | 0 | 0 | 27 |
| <i>Clethra</i> sp. | 0 | 0 | 4 | 7 | 5 | 14 | 0 | 0 | 9 |
| | | | | | | | | | 3682 |

* Values have been multiplied by 10 to compensate for the smaller area sampled.

through the middle two-thirds of the side of the cone. Disturbance was less there than at the base and summit. In the plots all trees an inch or over in diameter (as measured four feet from the ground), were counted and grouped in several size classes. Trees under an inch, and shrubs, were tabulated in plots 2 by 5 meters; and herbs in plots one-half by 2 meters. The small plots were always located in the one next larger in size, in a predetermined corner. Results of these studies are given in tables I and II. An indication of the importance of a tree species in a community is its presence in many size classes, with a high density and frequency for each class. On that basis *Quercus*, four species collectively, occupies first place among trees; *Pinus* is second, and *Arbutus* third. *Symplocos prionophylla*

Hemsl. and *Taonabo Pringlei* Rose, though they have high densities, are small trees and only subordinate members of the community. *Pinus* contributes the tallest and most conspicuous members of the forest. *P. pseudostrobus* is the more important of the two species in the plots; it has the greater density and is present in all size classes. Economically it is said to be superior to *P. leiophylla*, both as a lumber tree and as a turpentine source. Trees of other species are all small and are subordinate members of the community.

Ten species of shrubs were present, the two most important being *Arctostaphylos* and *Fuchsia michoacánensis* S. & M. *Coriaria thymifolia* H. & B., number three in terms of density, has a rather low frequency, 36 per cent, which indicates it is not widespread, but grows in colonies. *Salvia longispicata* M. & G. and *Russelia polyedra* Zucc. are as well distributed as *Coriaria* but each is only half as dense. It is worth noting that only three of the ten shrubs in the plots were included in the list of those considered to be important throughout the region. This may mean the other seven are confined to forests with considerable hardwood present, or it may mean that they have been killed out of other forests by the volcano. The first explanation seems more likely.

There was an unimpressive number of herb species in the plots, only 14 species, and those in small numbers. Frequency is also low in all cases. First two places are taken by grasses and third by a fern. A heavy canopy of trees and shrubs which overshadowed most of these plots probably inhibited the growth of more herbaceous ground-cover.

Rate of growth of pines.—Increment cores were taken from 65 pine trees, *Pinus pseudostrobus* and *P. leiophylla*, located in 18 different stations, as shown in figure 2. The trees selected were generally of moderate size, between about 5 and 12 inches in diameter. One station which furnished three trees was in the

TABLE II. Density and frequency of shrubs and herbs on the south side of a cinder cone near San Lorenzo. Angle of slope about 38 degrees. Values are based on an area of 140 square meters. Shrubs tabulated in fourteen 2 by 5 meter plots; herbs computed in fourteen plots one-half by 2 meters

| | Density* | Frequency |
|---|----------|-----------|
| Shrubs | | |
| <i>Arctostaphylos rupestris</i> | 167 | 86% |
| <i>Fuchsia michoacánensis</i> | 102 | 93 |
| <i>Coriaria thymifolia</i> | 92 | 36 |
| <i>Ceanothus coeruleus</i> | 68 | 50 |
| <i>Salvia longispicata</i> | 44 | 36 |
| <i>Russelia polyedra</i> | 41 | 36 |
| <i>Cologania biloba</i> (Lindl.) Nichols | 39 | 57 |
| <i>Xylosma flexuosum</i> Hemsl. | 8 | 7 |
| <i>Crocalaria pumila</i> Ort. | 6 | 21 |
| <i>Cestrum terminale</i> var. <i>latifolium</i> | 4 | 7 |
| | 571 | |
| Herbs | | |
| <i>Bromus pendulinus</i> Sessé | 210 | 36 |
| <i>Stipa mucronata</i> HBK. | 190 | 43 |
| <i>Cystopteris fragilis</i> (L.) Bernh. | 150 | 7 |
| <i>Ranunculus</i> sp. | 120 | 21 |
| <i>Passiflora</i> sp. | 90 | 7 |
| <i>Trifolium amabile</i> HBK. | 70 | 14 |
| <i>Physalis subintegra</i> Fern. | 70 | 14 |
| <i>Adiantum Poiretii</i> Wikstr. | 60 | 7 |
| <i>Cynodon dactylon</i> (L.) Pers. | 50 | 7 |
| <i>Lupinus elegans</i> HBK. | 50 | 7 |
| <i>Pteridium aquilinum</i> (L.) Kuhn | 40 | 7 |
| <i>Onosmodium strigosum</i> Don. | 20 | 14 |
| <i>Cyperus flauus</i> (Vahl.) Nees | 10 | 7 |
| <i>Begonia balsmiana</i> Ruiz | 10 | 7 |
| | 1140 | |

* Multiplied by 10 in case of herbs to compensate for smaller area.

upper pine zone; all others were in the pine-oak zone.

The cores showed the annual diameter increment of the pine trees to be rather "moderate" in amount. The maximum diameter increase for any tree for a year was 24.4 mm. The minimum increase was 2.8 mm.; the average for all trees was 8.5 mm.

Succession and climax. — Indications are that the climax forest in the pine-oak zone is one in which deciduous trees make up a considerable part of the population, perhaps half of the large trees and even more of the small. In the lower strata such forests are dense but at crown height they are rather open. Areally this type of forest is much less extensive than one in which pines are the important and, sometimes, almost the only trees. This second type appears to be in a subclimax



FIG. 5. Mixed forest on southwest facing slope of small cinder cone a half mile west of village of Carúpo. Largest trees are oaks. Dense shrub stratum; upper strata are open. Note epiphytes.



FIG. 6. Pure stand of pines (*Pinus pseudo-strobus*) in an abandoned field about a mile north of village of Angáhuán. Ash about 10 inches deep. Trees 10 to 12 feet tall. July, 1945.

condition. Three evidences substantiate these opinions: 1. There are small areas, such as found in some of the plots of the statistical studies, or that illustrated in figure 5, in which a majority of the trees are hardwoods. Such areas are almost without exception on steep slopes of cones, or other places not easily accessible to woodcutters and grazing cattle and sheep. 2. Large oaks are found sparingly but widely distributed. 3. Pines are the pioneer trees in abandoned fields and pastures. The seedlings grow rather thickly and seem to succeed under conditions of disturbance. Figure 6 shows a stand of pines in a field which has apparently been abandoned for some reason. Some of these trees were ten to twelve feet high. In forests the pines are often even-sized and may have all started about the same time in an abandoned field or, following disturbance, in a forest.

Most of these areas are subject to considerable disturbance. Sheep, cattle, and burros are grazed wherever there is forage. Because of the uncertainty of land ownership which has prevailed, any area not actually in use seems to be considered open for grazing and timber cutting. Woodcutters travel miles for firewood which they haul on burros, or to hew railroad ties which are transported by trucks. Oak wood is used in many parts of Mexico for making of charcoal, and may have been used for that purpose here too in times past.

*Fir and pine forests of upper elevations
on Cerro Angáhuán and Cerro
Tancítaro*

Some comparisons between the vegetation of Cerro Tancítaro, which had been studied extensively by Leavenworth ('46) in the two years just before Parícutin began eruption, and the vegetation of Cerro Angáhuán, which I observed in 1945, are of interest. Cerro Tancítaro is much older than Angáhuán, covers several times the area and is over 2,000 feet higher. Because of its greater age, and possibly also because of its greater size and larger water shed, Tancítaro is much more eroded. Consequently physiographic differences play a much bigger part in determining distribution of vegetation on Tancítaro than on Angáhuán.

On Cerro Angáhuán there are three forest zones. The pine-oak zone of lower altitudes gives way to a fir zone at about 9,000 feet and the transition is completed at about 9,400 feet. Besides *Abies*, which is the dominant tree, *Quercus* is also important in this second zone. Some of the oaks are five feet in diameter. Pines persist but are few in number. At about 10,000 feet *Abies* is rather suddenly reduced in amount and, while a few trees were observed up to the summit of Angáhuán, 10,594 feet, pines almost completely take their place. The pines are the same species as at lower altitudes. (Leavenworth ('46) states that on Cerro Tancítaro *Pinus montezumae* Lam. var. *rudis* Shaw, is common above 9,500 feet.) Oaks are absent. This forest is generally open and park-like, with grasses forming the main undergrowth. In a few places a low shrub, *Pernettya mexicana* Camp., grows densely.

Forest zonation on Tancítaro is essentially similar to that on Angáhuán, the chief difference being in the position of *Abies*. On Angáhuán this species is rather general between 9,000 and 10,000 feet, but is not present in important amount elsewhere. On Tancítaro it is

confined largely to valleys, where it descends to a lower altitude than on Angáhuán. On ridges it is scarce at any altitude.

It is evident that pine can, and does, grow from low altitudes up to the summits of these mountains. In some places they form only a minor part of the forest but that is because there oak and fir grow more luxuriantly. Both oaks and fir are more limited in their altitudinal ranges. Oaks grow to about 10,000 feet but no higher. Firs are nearly confined to a one thousand foot belt, between 9,000 and 10,000 feet, although in valleys they go lower. The upper limit of oak may be determined by temperature. There are no climatic records of any kind for these mountains but winters must be rather cold. Temperature may play a part in determining distribution of fir, although firs in general are quite cold resistant. The general distribution of fir here indicates that favorable water balance which results from reduced evaporation may be the critical factor in its success. Certainly its presence in valleys, but at the same time absence from ridges of the same altitude (Leavenworth '46), suggests the importance of water balance, or water balance and temperature differences due to air drainage. The fir belt is also the belt of most fog. My experience was that a fog blanket was the rule rather than the exception at this altitude, often being there when absent at lower and at higher altitudes. The importance of fog has evidently been appreciated by others, hence the name "cloud forest," which is applied to it.

ECOLOGICAL EFFECTS OF VOLCANISM

The volcano is affecting vegetation now, while it is still active, directly, in the way of destruction. But it will continue to influence vegetation indirectly for many years, probably centuries, after it ceases activity because of the way it is changing the environment. The indirect effects will be considered first.

Effects upon the environment

A new "soil."—Over a considerable area lava flows have effectively buried the old soil. In 1945 this area was about 5 square miles (fig. 2), but as the lava continues to flow it is greatly increased. The lava is basaltic rock, bare and sterile and incapable of supporting plant life until processes of weathering begin its decomposition and pioneer plants can become established. Revegetation on the flows will be slower than elsewhere and it may require centuries to effect a return to subclimax or climax forest, even if it is left undisturbed and is not used for agricultural purposes. It is probable that parts of the flows, especially such as are adjacent to large cinder cones, will have ash and soil washed or blown down onto them. Revegetation would take place more rapidly under such conditions.

The main cinder cone of Parícutin covers about a square mile. Its cinders are sterile, inorganic matter, similar in composition to the lava of the flows, and vary in texture from dust to boulders, most being of the size of sand and gravel. Revegetation of the cone cannot commence until activity ceases or at least is very slight. It will need to start with plants which are capable of living in such sterile soil, possibly thallophytes or bryophytes.

Extending beyond the cinder cone are a few square miles of area where ash (material small enough to be wind blown, see fig. 7) is so deep that all influence of the old soil is lost, and here too revegetation, starting with pioneer plants, will be necessary.



FIG. 7. Ash surface devoid of vegetation. Ripple marks are result of wind. September, 1945.

Thickness of ash.—Many measurements of the thickness of the ash were made in most parts of the area. It was done by making a cut with a shovel to the old soil surface and then measuring vertically along the cut. These measurements in inches, recorded at the places where made, and also iso-lines of ash depth are given in figure 2. The area south and west of the volcano is poorly investigated because that runs up into Cerro Tancítaro where work of this type is difficult because of erosion; records there would be extremely unreliable. No measurements of ash depth were made on flows.

In general there was a decrease in depth of ash with increase of distance from the volcano, as would be expected. This decrease is much less rapid to the south and west than it is to the north and east. For example, at the summit of Tancítaro mountain, which is about 6 miles away, ash was 14 inches deep, and 6 miles in the opposite direction, 2 inches. The prevailing winds which blow from the northeast are undoubtedly responsible.

The variation in depth of ash is often not uniform and gradual, and there may be a considerable difference between that of two spots quite near each other. Such discrepancies may be partly the result of the way the material was deposited by the wind, but it is more likely that erosion by water, after deposition, is responsible. As is shown below, erosion goes on quite unchecked during the rainy season.

Krauskopf and Williams ('46) present a generalized figure in which are shown with closed iso-lines the 6 inch, 1, 2, 3, 4, 5, and 10 foot ash depths, as of May, 1945. There is general agreement between their figure and the more detailed measurements recorded here, and the two sets of data complement each other nicely.

Erosion.—Erosion by water would always be considerable in such a mountainous region, but since volcanism began it has been increased manyfold. Much vegetation has been destroyed and no longer exerts its binding effect. The character of the ash is such that it "invites"

erosion. It is generally fine in texture and quite unconsolidated, and during a heavy rain the surface layer turns to a mud which flows away in sheet erosion. This mud coalesces into mud streams which flow down the gullies and into stream channels. Specific gravity of the flowing mud is nearly 2.0.

During the dry winter season ash is blown into dense dust clouds. The general result of several months of blowing is that the surfaces of ash fields are smoothed and evened. Early in July ash fields were somewhat eroded and dissected by water action but not nearly as much as by the middle of September after they had been subjected to two and a half months more of action by water. In September there was scarcely a square meter of surface left undissected on slopes (fig. 8). Lowdermilk ('47) estimated that about one-third of the ash which had fallen on slopes up to August, 1945, had already been moved into valleys.

The drainage pattern of a part of this area has been changed. Lava flows have cut across and filled some stream channels (fig. 2). Now, upon reaching the lava, streams are ponded and drop their sediments. There are numerous playas, formed in that way, east, south, and north of the lava flows. Debris has accumulated to a depth of many feet and consists of a great mixture of ash, old soil, leaves, branches of trees, logs, and disseminules of many plants. This should form a fertile spot for plant growth in the future. Streams whose upper courses have been blocked by lava flows have cut new channels along the west edge of the lava and then continue below in their former channels, where these have not been filled in.

*Direct effects of the volcano upon
vegetation*

Up to the date of this study direct effects had been largely in the nature of destruction, varying from complete elimination of all plants in areas buried by the cinder cone, deepest ash fields, and lava flows, to partial destruction where ash



FIG. 8. Severely gullied ash deposits estimated to be 30 to 40 feet deep, with tops of large pines protruding. One-half mile west of volcano. August, 1945.

was shallower, to less and less influence with increasing distance from the volcano.

Lava flows.—After emerging from their orifices the aa lava flows moved quite rapidly, during the present study, in narrow streams for a short distance. One flow observed at intervals over a period of several days, about an eighth mile from from its origin, was moving on an average of 15 feet per minute. That speed was faster than the average but by no means the maximum. Farther away from the orifice the lava spread into wider streams and the front was often an eighth or quarter mile across. The speed was then much reduced, being only a few feet per hour, or even per day.

Attention was given to moving flows to learn how they damage plants: whether the living plants are burned outright, whether radiant heat from the front of the flow kills them, and whether mechanical breakage is important. Observations were made along the margin of active flows and also of flows which had been

"dead" for a considerable time. An active flow which was moving into a forest was observed for about three hours. The flow was there about a mile north from its source and advanced, on an average, about six feet during the time. Over a hundred oaks and more than forty pines were overtaken by the flow during the three hours. In most instances the trees were bent away from the flow by the material pushing against the trunks and then they were buried. No instance of burning of such trees was seen. Rarely the tree fell toward the flow and then it usually burned because it came in contact with hot lava exposed when cooled pieces fell away from the front. We saw only one tree in actual process of burning. Quite often the tree was not moved from its position and the lava piled around it as it remained standing. No burning of such trees was seen.

At first thought it might seem impossible for an aa lava flow to move around and over trees without burning them but the explanation is comparatively simple. When flows move slowly there is ample time for surface material, both front and top, to cool. This cooled lava continually breaks from the upper front as the flow advances, it falls to the foot of the flow, and is then over-ridden. Hence there is an insulating layer of cold rock at the front and base of the flow, and only rarely does hot lava of the inside of the flow reach the extreme front. It is of course likely that when a flow has advanced a considerable distance over trees that they would be burned and that even the cooled rocks would be remelted.

The "dead" flow whose effects are described here had been active in 1944, (about a year before these observations). It was studied at a site about five miles from its source, considering the circuitous route it had taken, at a point adjacent to the Headquarters Cabin (fig. 2). The flow averaged about fifteen feet in thickness. The edge where observed varied from the vertical to a low angle of about 20 degrees. The ash blanket in this vicinity

was about two feet thick. For about a mile along the edge of the flow observations were made on the condition of all plants and plant remains which were within six feet of the flow. Any plant farther away was assumed to be beyond the influence of the flow. Each plant was put into one of three categories, according to its condition: 1. Apparently unharmed by the flow. 2. Injured, but making a recovery (usually partly or entirely killed above ground but sending out new growth from stem or roots). 3. Apparently dead. The results are summarized in table III.

TABLE III. *Effects of proximity to a stationary lava flow edge on plants. All plants were within six feet of the flow which had cooled a year before observations were made*

| | Apparently unharmed | Injured but recovering* | Apparently completely dead |
|------------------------------------|---------------------|-------------------------|----------------------------|
| Trees | | | |
| <i>Alnus jorullensis</i> | 1 | 0 | 0 |
| <i>Arbutus xalapensis</i> | 1 | 4 | 0 |
| <i>Crataegus pubescens</i> | 12 | 7 | 12 |
| <i>Pinus leiophylla</i> | 4 | 1 | 0 |
| Shrubs | | | |
| <i>Bouvardia ternifolia</i> | 2 | 1 | 0 |
| (Cav.) Schlecht | | | |
| <i>Rosa</i> sp. | 1 | 0 | 0 |
| <i>Smilax moranensis</i> M. & G. | 0 | 2 | 0 |
| <i>Symphoricarpos microphyllus</i> | 2 | 1 | 0 |
| Herbs | | | |
| <i>Cynodon dactylon</i> | 2 | 0 | 0 |

* Usually partly or entirely killed above ground and sending out new growth from stem or roots.

The flow happened to pass through the edge of the village of San Juan and the vegetation was not all native forest. Most of the *Crataegus* had probably been planted. The rose was certainly a cultivated plant. This latter was a large plant with a stem about two inches through at the base. Even though the lava was touching it the plant was healthy, showed no sign of damage and bore quantities of beautiful blossoms. Figure 9 shows the lava flow and the character of some of the vegetation that remained.

These observations indicate that the effects of aa lava flows upon plants, particularly trees, are largely in the nature of mechanical injury rather than burning or killing by radiant heat. Contact of a lava flow with a plant, or even partial burial, if the plant is not crushed, may not result in its death.

Ash Deposits.—Studies were made of the vegetation of the ash fields in relation to environment. These included: keeping a record through the season of plant species found in the areas; excavations of the root systems and buried stems of many plants; and the plotting of a map of the limits of plant survival, that is, points closest to the volcano where plants remained alive. All these studies were carried on at the 34 stations indicated in figure 2, and plants census records were kept at many more than the 34 sites. The following discussions are based upon these studies and the measurements of ash depths which are given in figure 2.

1. Vegetation in different directions from the volcano

Indications are that several factors may be responsible for the destruction of vegetation in ash fields. Sometimes it is rather evident which are effective, and again one cannot know. The first and

most obvious cause is complete and continued burial. Others are partial burial which would reduce access of oxygen to the roots; breakage because of the weight of ash upon the plant; starvation and suffocation because of a coating of ash over the leaves or stems which would reduce light intensity and clog stomata thereby reducing photosynthesis, or starvation because of the prolonged absence of leaves. Possibly, when the volcano was younger poisonous gases may have been a factor, but by 1945 nothing survived near enough to the main vents to be much affected by that.

It very early became evident that there was rather poor correlation between survival of vegetation and distance from the volcano. Plants have been harmed much less north and east than at equal distances south and west. This suggests a relation between vegetation and depth of ash since it has been shown that ash is deeper to the south and west. But here again the records do not show more than a general relationship. Vegetation is generally in better condition east and northeast than west and southwest at comparable depths of ash. This suggests that accumulation of ash about the base of a plant is not the only factor at work here. Effects of continued presence of a layer of ash on the



FIG. 9. Edge of a "dead" lava flow which had stopped advancing in this direction about a year before. Photo taken about a half mile southwest of headquarters cabin. This flow was studied to learn its effect upon marginal vegetation.

plant leaves seem to be even more important. Prevailing winds for much of the year are from the east or northeast, hence vegetation to the west is subjected to an almost constant shower of ash and has little chance to recuperate. Ash is blown east and northeast but not for long periods and plants can recover between times.

The approximate limit of living vegetation is indicated in figure 2. At the outer limit of this area ash varied between approximately 4 and 6 feet in depth. It is not possible to indicate an exact line, beyond which there was no living vegetation. There were many small areas outside the line where all was dead, and there were scattered living plants inside. For example there were a few pines inside sufficiently alive to warrant the taking of increment cores.

2. *Species present in different depths of ash*

The most interesting studies of the ash fields were in the large area outside that of total destruction. It has already been stated that there was not a close relation between vegetation and depth of ash; nevertheless it seems worth while to present this comparison for what it is worth as a matter of record. Most of the observations on vegetation upon which it is based were made north, east, and south of the volcano. There is closer correlation between vegetation and depth of ash in these directions than west of the volcano where starvation and suffocation played a bigger part in killing of plants. The information is summarized in table IV.

(a) *Trees*

(1) *Pines*

No attempt is made here to differentiate between pine species as they reacted rather similarly. For convenience of record the pines have been considered in five size classes. First to succumb in ash were small ones, those under an inch in diame-

ter. They were generally dead where ash was about a foot or more deep. In some places however this size was all killed in 8 inches of ash. Next to be killed were those an inch or over, but under three inches; then those 3 to 5 inches. Almost as easily killed as those in group three were the big trees, those over a foot in diameter. They suffer exceedingly from breakage; their branches are brittle and cannot withstand a heavy load of ash. Generally about 24 inches of ash was needed to kill the big trees but many were dead in 10 inches. The last pines to succumb were those having diameters between 5 inches and a foot. They are large enough for the main stem to resist strong bending and burial, yet the branches are flexible enough to yield and not break (fig. 10). The maximum depth of ash in which a pine survived was about seven feet.

Often in ash between 8 and 20 inches deep small pines were bent over and their tops buried. Some of them subsequently died, but a good many continued to grow. Upper branches of the latter group grew rapidly if the tree was healthy, and altered their polarity and symmetry to produce vertical tree-like growth, but, inasmuch as there were never adventitious roots from main stem or branches to furnish extra nourishment, aeration, and support, it is unlikely that many of the branches can grow to tree size. No branch or tree top which was buried to its tip end remains alive. (It may be mentioned here that adventitious roots were found on no trees buried in ash and in only one shrub species were there individuals with adventitious roots).

There is no evidence that among those pines which remained alive there has been more than a modest decrease in rate of growth during the two and a half years of volcanic activity as compared with the years just preceding. Numerous trees in the vicinity of the Headquarters Cabin, where ash was about 20 inches deep, grew more in height during each of the years of volcanism than in the year just before. It may be that killing of most of the under-

TABLE IV. Average maximum depths of volcanic ash in which plants were able to survive. Includes plants north, east, and south of Parícutin Volcano

| Depths of ash in inches | Trees | Shrubs | Herbs |
|-------------------------------|---|---|---|
| 70 | <i>Quercus</i> | | |
| 60 | <i>Alnus</i> | | |
| 50 | <i>Pinus</i> (5"-12" diam.) | <i>Cestrum, Smilax</i> | |
| 40 | <i>Crataegus</i> | | |
| | <i>Arbutus</i> | | |
| | <i>Pinus</i> (Over 12" diam.) <i>Pinus</i> (3"-5" diam.) | | |
| 30 | | | <i>Argemone platyceras</i> Link & Otto <i>Mimosa</i> |
| | | <i>Symphoricarpos</i> | <i>Mirabilis longiflora</i> L., <i>Pteridium aquilinum</i> |
| | <i>Pinus</i> (1"-3" diam.) <i>Fraxinus, Prunus</i> | <i>Bouvardia</i> | <i>Stipa</i> |
| 20 | | <i>Baccharis, Fuchsia Pringlei,</i> <i>Cortaria, Senecio platensis/olius</i> | <i>Cynodon, Digitaria, Asclepias neglecta</i> Hemsl. <i>Ceranium, Senecio affinis</i> Stutz. <i>Erigeron, Euphorbia</i> DC. <i>Solanum michoacanum</i> (Bitter) Rydb. <i>Palisota</i> Zucc. <i>Bromus pendulinus</i> DC. <i>Valeriana procera</i> HBK., <i>Erigeron scoposus</i> DC. <i>Desmodium millicam</i> (HBK.) DC., <i>Ipomoea</i> sp. <i>Salvia frutescens</i> HBK., <i>Sporobolus indicus</i> (L.) Br. <i>Fuchsia fulgens</i> DC. |
| | <i>Abies</i> | <i>Amelanchier, Salix</i> | |
| | <i>Pinus</i> (Under 1" diam.), <i>Tilia</i> | <i>Arctostaphylos</i> | |
| 10 | | | <i>Galium mexicanum</i> HBK., <i>Galium trifidum</i> L. |
| | <i>Clethra obovata</i> Hook. & Arn., <i>Symplocos</i> | | |



FIG. 10. Pine forest about two miles northwest of volcano, showing effects of 46-inch ash deposit. Most trees have broken branches; some have tops broken also. A few medium sized trees (most resistant size class) remain alive. August, 1945.

growth actually improved growing conditions. The average annual diameter increase, during the period of volcanism, of the 65 pines bored (fig. 2) was 4.2 mm. The average for each of the ten years preceding was 6.74 mm. This is not a great difference considering that many of the trees occupy positions close to the volcano and are constantly subjected to conditions that may eventually lead to their deaths. Some of the decrease in growth rate is normal slow-down that comes with greater age and diameter.

(2) Oaks

Oaks are among the most resistant to volcanism of all plants found here. Because of their small numbers at the lower altitudes and their scattered occurrence it was not possible to correlate their condition with depth of ash as completely as was possible for the pines. There were oaks with at least vestiges of life in ash as deep as was possible to measure—226 inches. Such a "vestige" might be only a green branch on a tree which otherwise

seemed quite lifeless. Probably many with such bits of life in evidence never recovered enough to retain it for long. As in the pines, a branch or tree top buried to its tip never lives. Also like the pines, the medium sized trees, those between 5 inches and a foot in diameter survived best. An indication of the hardiness of the oaks is seen in the fact that in one-fifth of the ash field sites where living oaks were studied the ash was over 6 feet deep. (See fig. 11.) Usually, however, there were few alive if ash was two or three feet deep, and large trees generally failed to survive in 20 inches.

(3) Other Trees

Madroña, a small tree and minor member of the community, withstood burial rather well. Usually it was dead in two or three feet of ash, but several living specimens were seen in 78 inches, one in 95 inches, and another in 118.

Crataegus is usually low and quite branching from the base, and so not well adapted to withstand deep accumulations

of ash but it did well for its size. It was often alive in ash up to 40 inches. It is a common habitant of fence rows where it may be the only plant left alive. Again, any branches completely covered die. Here, breakage of branches does not necessarily result in death of the tree, as in pines, because branches continue to function when partly broken off.

Alnus is small but has wonderful capacity for recovering from deep burial. After all its branches and leaves are gone, buds may come directly from the old trunk and the plant starts to grow again. It is not known if such recovery is more than temporary.

(b) Shrubs

Probably the most abundant shrub in ash-covered areas is *Baccharis*. It is most characteristic of fields but is also present in pine woods. Several plants which were

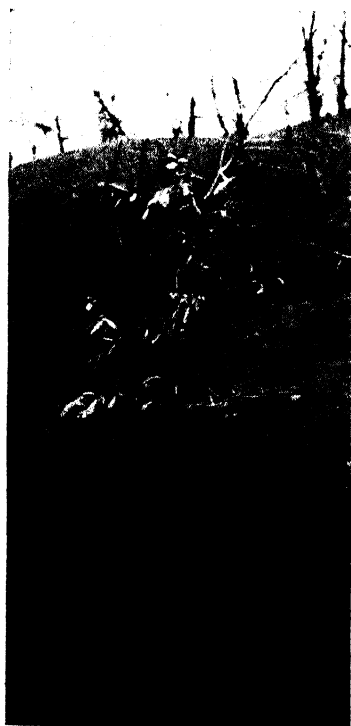


FIG. 11. A living oak tree with 6 feet of its body buried by ash and 7 feet above, unburied. July, 1945.

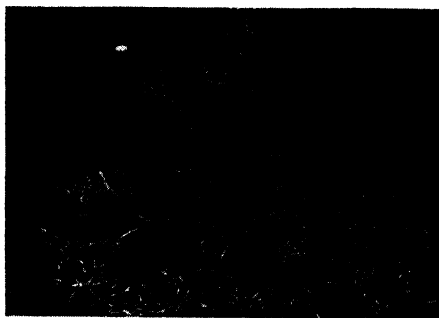


FIG. 12. *Baccharis* shrub with Bermuda grass (*Cynodon dactylon*) around it. Ash about ten inches deep. September, 1945.

partially buried were excavated (fig 12). All of them which were excavated had adventitious roots growing from the buried parts of the stems. This species was growing successfully in ash up to a depth of 22 inches and was one of the few plants which were spreading.

After *Baccharis* are two other shrubs, about equal in importance. In both fields and woods *Cestrum* is common although it never grows in closed stands. At times it is the only shrub. It has a capacity for continuing growth when only a small part extends above the ash. One plant was seen in 50 inches and two others in 46 inches of ash. The plants were healthy looking and bore quantities of fruits and flowers. *Fuchsia Pringlei* is a shrub in pine woods where it sometimes forms almost a continuous ground cover. This species is said to grow to a height of several feet but here it was usually not over two feet. It grew in ash to 22 inches. Excavations of several indicated that the parent plant was killed back, in all cases, to the old soil level and that it then resprouted.

A plant which is striking in appearance because of its red flowers which stand out against the background of ash is *Bouvardia*. All that were excavated had been killed back to the old soil and then sprouted from the old stem base. It generally survived successfully in ash which had accumulated to a depth of 20 inches,



FIG. 13. Small field near base of Cerro Angáhuán. Parícutin erupting in distance. Ash about 8 inches deep. Bermuda grass covers about a third of ash surface and has continued to grow all during period of eruption. August, 1945.

and one was found where the ash was 29 inches deep.

(c) Herbs

Herbs most important in the ash fields, from the standpoint of surface coverage, were grasses. Chief of these was Bermuda grass, *Cynodon dactylon*. In fields with not over 10 inches of ash this grass covered as much as half of the surface area (fig. 13). In a field with 15 inches of ash this grass covered about 10 per cent of the surface. Where ash was deeper, up to 20 inches, it persisted but only around stumps, bushes, and trees



FIG. 14. Bermuda grass grown up through nearly two feet of ash at base of a dead pine tree. September, 1945.

(fig. 14). It is not evident why grass would grow there and not elsewhere, but perhaps it obtained a degree of protection against wind and water erosion, or possibly received some special nutrition from dead fragments of bark. Several clumps of the grass were excavated and rhizomes were traced all through the ash down to the old soil surface. It is quite evident that the plants grew throughout the whole eruption. Where established the grass was spreading vegetatively. In a few places it had started to grow in old soil in the bottoms of small gullies in ash. In such cases it helped to control erosion. *Digitaria velutina* (Dc) Hitch., crab grass, has growth habits quite similar to those of Bermuda grass. It occupied habitats similar to those supporting Bermuda grass but there was less of it.

Stipa mucronata was widely distributed in areas where ash was not over 22 inches deep. The plants were scattered in the usual bunch grass manner. It is believed that *Stipa* propagated vegetatively from old plants also.

Several dicotyledonous herbs were found in the ash fields. These either grew throughout the period of volcanism or else they sprouted from parent plants which were killed back to the old soil level.

First members of these dicotyledons are *Argemone platyceras* (fig. 15) and *Mirabilis longiflora* (fig. 16). They are large herbs and the most conspicuous plants in the fields. They produce large white flowers which stand out against the dark ash background. The deepest ash in which they were found was 29 inches for *Argemone* and 24 for *Mirabilis*. Other important herbs of the fields are *Asclepias neglecta* and *Erigeron scaposus*, in ash to 20 inches, and bracken fern (*Pteridium aquilinum*), in ash to 24 inches.

Century plant (*Agave*, sp.) a monocot which was probably originally planted in every situation where seen, deserves special mention because of its ability to retain life, even if completely buried for a long time. Plants may be buried under ash for a year or more and then, if uncovered through water erosion, appear quite alive and ready to continue to grow.

PROPAGATION BY SEEDS

Consideration has been given thus far largely to plants which were present when



FIG. 16. *Mirabilis longiflora* grown up through about 16 inches of ash. September, 1945.

volcanism began and then continued to grow without interruption, or were killed back and grew again from sprouts. Reproduction by seeds is just as necessary in these plant communities as vegetative propagation, for it will be only by means of seeds that many species which have been completely killed out can come back and it is only by seeds that some species can increase in numbers when established.

There are two potential sources of seeds for the ash covered areas: seeds buried under the ash in the old soil, and those which had been dispersed after volcanism started and were therefore deposited at various levels in the ash. The problem of seed germination is associated with kinds and amounts of nutrients and possibly inhibitors which may be present in the raw ash. At the present time these problems remain largely unsolved.

Seeds in old soil

Undoubtedly many seeds were buried when volcanic ash started to fall over the area in 1943. Some of these seeds might be expected to germinate when moisture conditions are favorable, and, if the ash layer is not too thick, one would expect seeds to be able to germinate and seedlings to push through and reach light and hence become established. But apparently lack of aeration or some other influence prevents that, for seedlings do not occur. Constant watch was kept for seedlings which had germinated in the old buried soil, but none was found, not even in ash as little as two inches thick. (See the

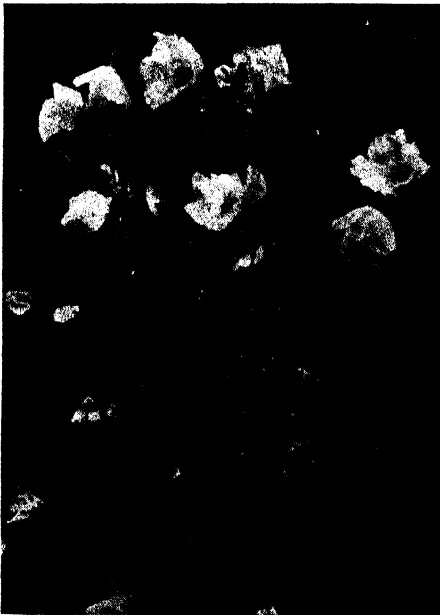


FIG. 15. Prickly poppy (*Argemone platyceras*) grown up through about 20 inches of ash. September, 1945.

barren condition in fig. 7, taken in an old field where ash was about 3 inches deep.) Presence of carbon dioxide in inhibiting concentration or lack of oxygen supply are suspected, but it is not known what prevents germination and growth of seedlings through ash. Where erosion removed the ash a good crop of weeds usually soon appeared, indicating that viable seeds were present.

Seeds in new ash

Two instances were observed in the field of germination of seeds which were disseminated during the period of volcanism. About a dozen pine seedlings, probably *Pinus pseudostrobus*, were found five miles east of the volcano where ash was between 6 inches and a foot deep. The seeds had germinated at a depth of about four inches below the surface. When seen the seedlings were well established, parts above ground were six to eight inches tall, and roots had penetrated down into the old soil. *Baccharis* seedlings were also found. A large clump with hundreds of seedlings had started in about 22 inches of ash. When seen the tops were about five inches tall. Seeds had germinated about a half inch below the surface of the ash. Roots of these seedlings had not yet reached the old soil surface and ultimate success was uncertain. Some of the ash in which they were growing appeared to have been brought by water and so may have been leached of toxic substances, and also under the circumstances, one could not be sure there was not some organic matter mixed with it.

GROWING OF MAIZE IN ASH FIELDS

Erosion of fields by water and killing of plants by ash which settled as a film on the leaves apparently discouraged the Tarascan Indians so much that in 1945 almost no corn was grown in the area of this study. In most places it would have been impossible as well as impractical to plant. But small plantings in and near the village of Angáhuán indicated that

possibly not all fields were as unfit for use as their owners may have believed. Ash in Angáhuán averaged about 14 inches deep. A few optimists planted corn and were obtaining an average crop (fig. 4). Grains were planted very deep so roots of the plants could soon reach the old soil.

The success in Angáhuán indicates that hundreds of acres of fields lying idle were capable of producing corn. Observations indicated that a field with not over a foot of ash, which lies to the windward side of the volcano so it is not subjected to constant ash fall, and which is in a position to avoid erosion and silting by water, could profitably be planted to corn. The grains should be planted 6 or 8 inches deep. It is likely that after a year or two of cropping, yields would be as good or better than formerly because of the availability of new nutrients released from the ash.

SUMMARY

The new volcano, Parícutin, which was born on February 20, 1943, in the state of Michóacán, Mexico, began at once to change the character of vegetation in a variety of ways: by complete destruction, by selective killing, by changing the growth rates of plants that remained, and by providing a new mineral stratum which would affect germination and seedling establishment. Field studies for this report were carried on in the summer of 1945. They consisted of a reconstruction, through studies of unaffected forests nearby, of the ecologic character and floristic composition of the vegetation as it had been before volcanism started, and comparable studies of the affected vegetation after two and a half years of volcanic activity.

At the time of this study the summit of the main cinder cone stood about 1,500 feet above the original land surface (altitude 7,400 feet), the cone was a mile in diameter at the base, lava flows covered about five square miles, and hundreds of square miles of forest and fields were

mantled by wind-borne ash. Practically all the study was done in an area about 10 by 12 miles in extent, with the volcano near the center.

There are three main forest types in the region. Below about 9,000 feet altitude is a pine-oak forest. In the climax condition this forest contains a mixture of oak and pine, with oak probably in the majority. There is very little of the climax. There are three species of pine, the two main ones being *Pinus pseudo-strobus* and *P. leiophylla*. There are eight oaks, two being most abundant, *Quercus orbiculata* and *Q. magnoliaefolia*. Pine reproduces more successfully in open woods and pastures and abandoned fields. Since disturbance is so common in this country where land is scarce, pine has come to be the main tree in most parts of this zone. Between 9,000 and 10,000 feet, *Abies religiosa* is dominant. Above 10,000 feet pines are again present and in almost pure stands.

Measurements of the thickness of the ash were made in many places in the study area and these are recorded on a map. The greatest depth it was possible to measure was 226 inches. Close to the main cinder cone ash was even deeper than could be measured.

The damage done by aa lava flows as they move toward and then overwhelm trees is not so much the result of excessive heat as of mechanical breakage. Even contact with a flow may not kill a plant, provided it is not injured mechanically. This is because surface lava cools quickly and serves as an insulation against the hot lava within the flow.

Several square miles of vegetation has been completely destroyed. The old soil had been buried so deeply by lava flows, cinders, and ash that its influence has been lost and revegetation will have to start upon the new volcanic materials.

Outside of the area of total destruction there had been selective elimination of plant species or of certain size classes of a species. Several factors, individually or collectively, caused this destruction:

burial, partial or complete; breakage because of the weight of ash upon the plant; starvation because of a coating of ash upon the plant or because of repeated destruction of leaves. Destruction of vegetation is correlated to a degree with depth of ash. However there is more destruction south and west of the volcano than north and east at the same depths of ash because prevailing winds keep plants to the south and west coated with ash.

Pines are sufficiently abundant through the region to permit a correlation between their survival and depth of ash. First to be killed are trees under an inch in diameter; next, in deeper ash, those from 1 to 3 inches, then those 3 to 5 inches, then those over a foot in diameter, and last those between 5 inches and a foot. Among those pines which have survived there has been little decrease in rate of growth during the years of volcanism as compared with the years just before, even among trees in deep ash.

Shrubs which have survived near the volcano have generally continued to grow all during the period of eruption. An exception was *Bouvardia*, which died back to the old soil surface and then grew up again from the stump. Herbs which have survived have generally been killed back first to the old soil surface but two grasses, *Cynodon dactylon* and *Digitaria velutina*, were able in many cases to keep ahead of the ash and grew all during the eruption.

In the summer of 1945 essentially the only plants in the area were the survivors from pre-volcanic times. There was scarcely any reproduction by seeds, a necessary process before bare areas can be repopulated.

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THE SURVIVAL OF WILD BROWN RATS ON A MARYLAND FARM¹

DAVID E. DAVIS

Department of Parasitology, The Johns Hopkins University

INTRODUCTION

The length of life of a wild animal is obviously of fundamental importance to the studies of ecology and management of the species. This paper describes investigations designed to determine how long Brown Rats (*Rattus norvegicus*) live under natural conditions. Although for rats the length of life in captivity is known, it is of little use in ecological work.

These studies of survival of rats were conducted near Baltimore, Maryland at a farm on which the chief activity was breeding and boarding race horses. The farm had about 50–60 horses, 10–12 cows, 10–20 pigs, about 100 chickens and ducks, and

3–4 dogs. Wild cats occasionally appeared and stayed for a few months. Skunks (*Mephitis mephitis*) passed through the barnyard occasionally and a Barn Owl (*Tyto alba*) lived in the biggest barn for 2 months. Rats and mice (*Mus musculus*) were abundant in all buildings.

The farm had 4 main buildings (figures 1, 2). A big barn, filled with hay, held the cows, work horses and some race horses, while two other barns each held about 20 race horses. The fourth building was a corn crib to which were attached horse stalls, a bull pen, and a machine shed. These buildings all needed repair and provided excellent shelter for rats.

There was an ample supply of food at all times. Feed for the horses was kept in wooden bins and placed in the feeding troughs once or twice a day. Feed for the cows was kept in open tubs and shoveled out to the feeding troughs. Water was available in pails at each horse stall.

¹ Contribution from the Rodent Ecology Project of the Department of Parasitology, School of Hygiene and Public Health, The Johns Hopkins University. The work reported in this paper was conducted under a grant from the International Health Division of the Rockefeller Foundation.



FIG. 1. Cow barn.



FIG. 2. Corn crib and machine shed on the left and horse stalls on the right.

Corn was kept in the crib until June when the supply was exhausted and not replenished. Game cocks were fed in the machine shed till July. Although the quantity of food was ample apparently the quality was not satisfactory since growth rate studies (Davis and Winsor, '48)

showed that the diet was deficient in some way.

The mortality of rats during the experiment was due to many factors. The hired men killed rats when opportunity arose; some children shot rats for sport; 3 of the dogs caught many rats; the va-

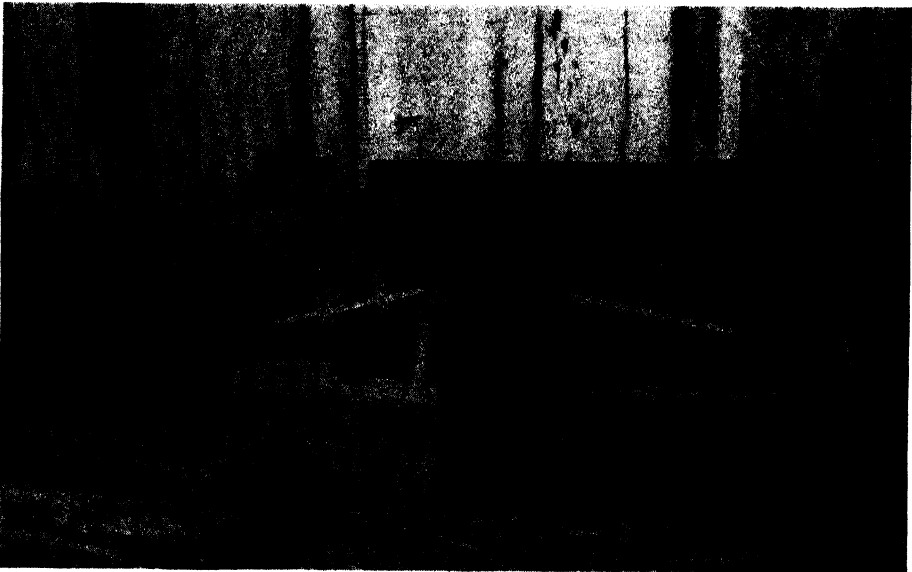


FIG. 3. Traps set at rat hole in foundation.

grant cats ate rats (88% of contents of scats was rat hair); the Barn Owl ate rats, some of which were carrion (34 pellets contained 22 skulls of rats and 31 skulls of other small mammals); the bacterium *Salmonella typhimurium* weakened many rats, some of which are known to have recovered; horses occasionally trampled rats to death; traps accidentally killed a few rats.

The rats were captured (figure 3) unharmed in box traps (Richter and Emlen, '45), marked by clipping toes according to a code system, weighed, sexed, and released at the location of capture. The traps were set in every available place but it was impossible to set traps in many good places because of interference by horses or cows. About 80-100 traps were set in alternate weeks. Trapping and releasing was begun on March 26, 1946, and ended March 15, 1947. From March 17-26, 1947, steel and snap traps

were used to kill and remove the rats. Since that time steel traps have been used at monthly intervals.

To analyze the survival data, the weeks are grouped together into biological seasons according to the precipitation and temperature as shown in the weekly hythergraph (figure 4). It will be noted that the weeks can be divided into fairly distinct seasons. Although possessing deficiencies, the use of biological seasons based on climate is better than the use of seasons based on the calendar. For example, the hibernal season of 1946-47 was very long (figure 4) due to an unusually cold, late spring. Hence the rats did not increase the rate of reproduction in 1947 until a month later than in 1946.

The marking and recapturing experiment was ended March 15, 1947, because the number of rats captured declined to such an extent that the work could not be profitably continued. Indeed only 23 rats

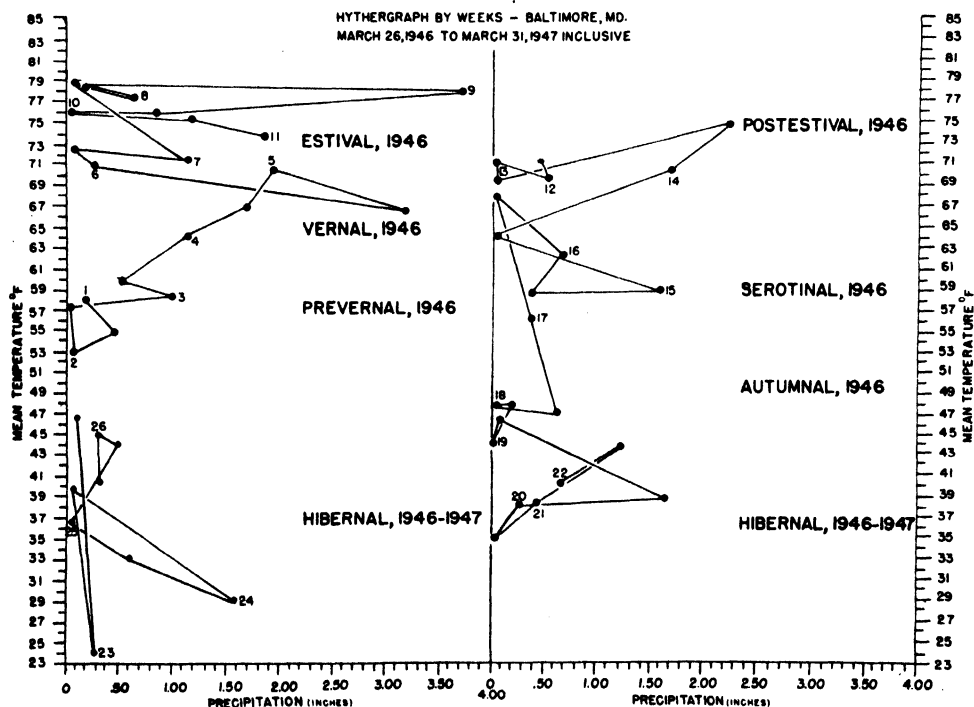


FIG. 4. Hythergraph showing temperature ($^{\circ}$ F.) and total precipitation (inches) for each week from March 26, 1946, to March 31, 1947. The numbers represent the periods (weeks) during which rats were trapped.

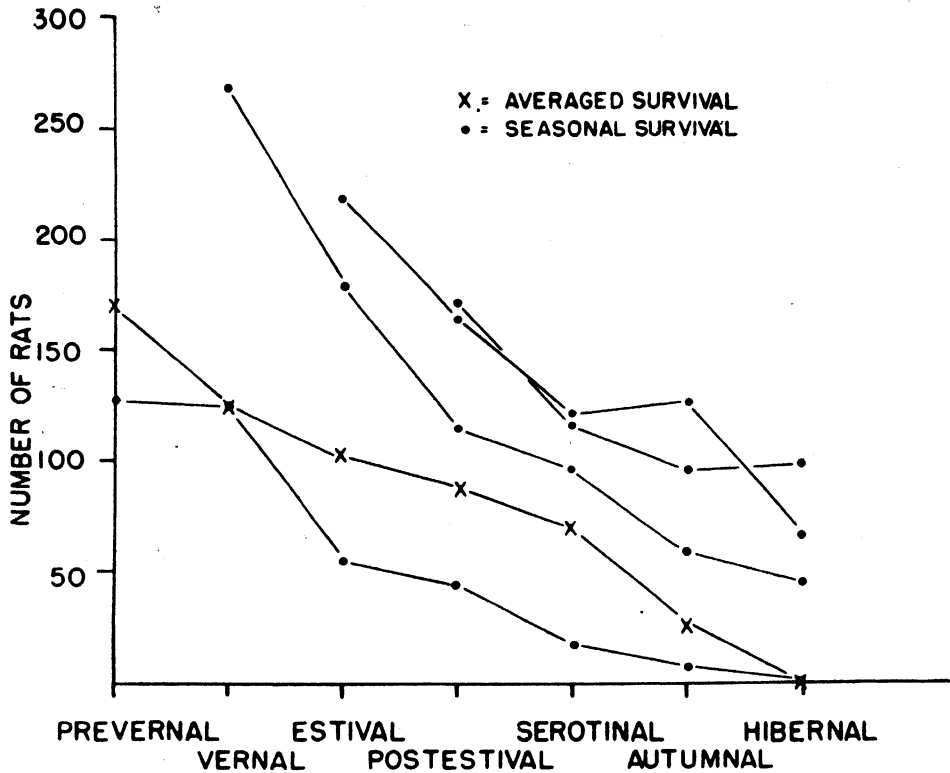


FIG. 5. Survival curves for rats marked and released in various seasons (dots) and averaged survival (crosses).

were captured with box traps in the 400 trap nights of the last period. In the next 2 weeks 150 rats were captured by the more effective steel and snap traps.

While the mortality of the rats on this farm was due to factors which are probably present on most farms, the survival is also dependent upon food and climatic conditions which may vary from farm to farm or year to year. For example, it is possible that the poor quality of the food reduced survival time and that the unusually late winter climatic conditions of 1947 influenced survival time. Therefore, because of these complexities, the survival data presented here cannot be hastily generalized for other regions or conditions but must await other investigations.

METHODS OF CALCULATING SURVIVAL

In order to obtain figures for the survival of rats on the farm it is first neces-

sary to obtain estimates of the population on the farm at various times. The method developed by Jackson ('39) for calculating the population by means of the ratio between the marked and unmarked rats was used. The populations were first calculated by using each week but in many weeks the number of recaptured rats was so small that great chance variation occurred. Hence the weeks were grouped into seasons and the populations of mature rats were calculated for each biological season. Jackson uses the principle that the population equals the number of individuals marked in one period multiplied by the number captured at a subsequent period and then divided by the number of individuals which had been marked in the first period and were recaptured at the subsequent week. Since Jackson's method is fully described in his paper, and since the details of calcu-

lation are not pertinent to this paper, the data necessary for calculations are relegated to an appendix.

The population (table I) increased in the vernal season, apparently due to reproduction, and then declined in part, at

least, due to a decrease in corn and chicken feed at the crib.

The method of calculating the survival of rats follows the procedure of Leopold *et al.* ('43), Green and Evans ('41), Buss ('46) in which the number of surviving

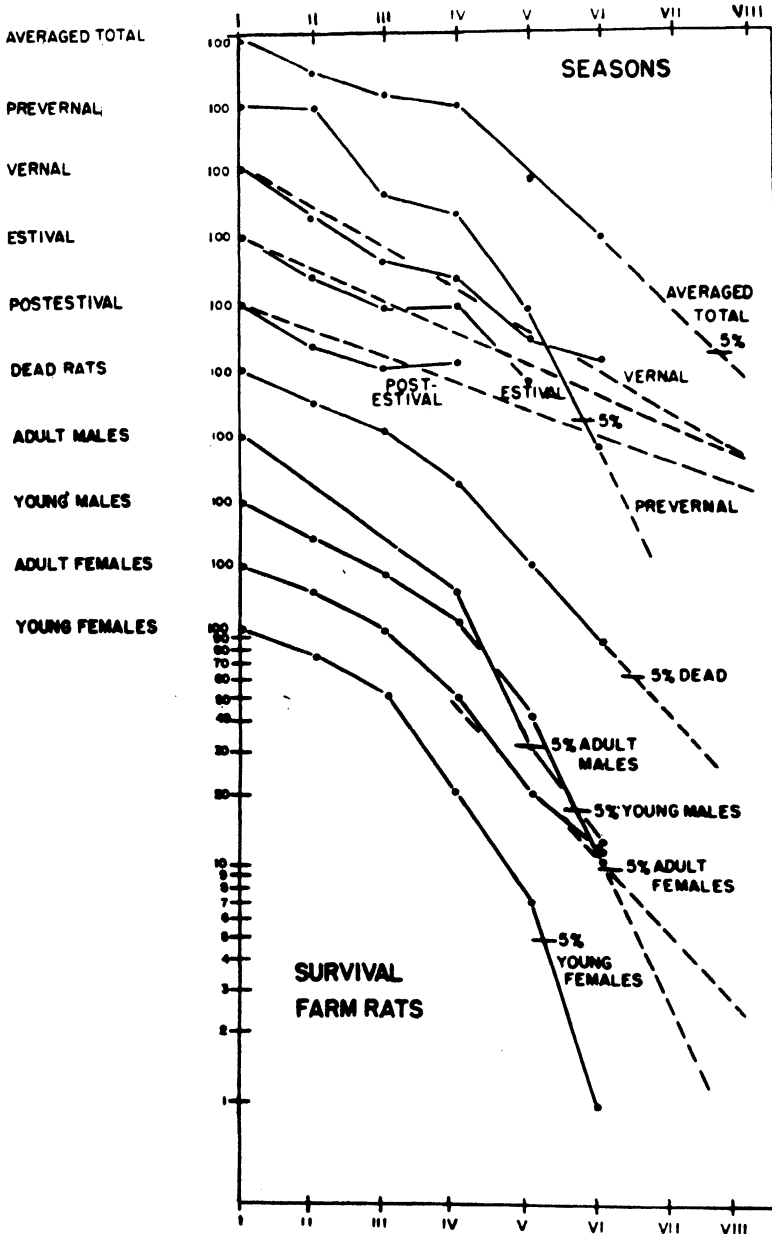


FIG. 6. Survival curves on semilogarithm paper showing survival of seasonal and age categories and 5 per cent survival time.

TABLE I. *Population of rats on farm*

| Weeks | Season | Dates | Calculated population | | |
|-------|-------------|------------------|-----------------------|-----------------|---------|
| | | | Positive method | Negative method | Average |
| 1-5 | Prevernal | March 26-May 2 | 605 | — | (605) |
| 7-11 | Vernal | May 14-June 15 | 1125 | 1162 | 1146 |
| 13-19 | Estival | June 25-Aug. 10 | 950 | 832 | 891 |
| 21-25 | Postestival | Aug. 20-Sept. 21 | 810 | 1012 | 911 |
| 27-31 | Serotinal | Oct. 1-Nov. 2 | 1050 | 740 | 895 |
| 33-37 | Autumnal | Nov. 13-Dec. 14 | 798 | 774 | 786 |
| 39-52 | Hibernal | Dec. 30-March 21 | — | 590 | (590) |

(marked) individuals captured is corrected for the uncaptured residue of marked individuals in the population. The basic data are presented in tables II and III, and the results in figures 5 and 6. For example, in the prevernal season 130 rats were marked and released (table II). In the vernal season 29 marked rats and 231 unmarked mature rats (total of 260 rats) were caught. Since the population in the vernal season was calculated to be 1146 mature rats, therefore 886 were not caught. Assuming that the ratio of marked rats (29) to caught rats (260) is the same in the captured (260) and uncaptured (886) parts of the population, then there were 99 marked rats which were not caught. The data for calculating the numbers of rats surviving by consideration of the untrapped residue are given in table II. These results are recorded in table III (rats not captured), added to the rats known to be alive (rats recaptured), to give the number of rats calculated to be alive (survivors). In order

to make possible a comparison of the seasons the survivals are calculated on a percentage basis in table III. To continue the example, from these calculations it is concluded that a total of 128 rats, marked in the prevernal season, were alive in the vernal season. Similar calculations were made for all seasons but the data for serotinal and autumnal seasons extend for only a short time and will not be discussed in detail. In order to get a summary figure for survival the categories of table III were totaled, giving an averaged figure for survival as if all 1036 rats had been marked at once and then found surviving at subsequent dates. Thus in table III of the 1036 rats marked in the experiment, 763 were alive one season after marking; 516 were alive 2 seasons after marking; etc.

For an understanding of survival the chronological age of rats should be known but it is not possible to determine the age of rats except by such physiological characters as weight, vaginal perforation, etc.

TABLE II. *Data for calculating survival of rats*

| Season of marking | Prevernal | Vernal | Estival | Postestival | Serotinal | Autumnal | Hibernal |
|-------------------------|-----------|--------|---------|-------------|-----------|----------|----------|
| Marked and released | 130 | 269 | 242 | 170 | 151 | 74 | (87) |
| Mature rats caught | 109 | 260 | 253 | 197 | 155 | 141 | 151 |
| Population ¹ | 605 | 1146 | 891 | 911 | 895 | 786 | 590 |
| Not caught ¹ | 496 | 886 | 638 | 714 | 740 | 645 | 439 |
| Vernal | 29 | — | — | — | — | — | — |
| Estival | 16 | 52 | — | — | — | — | — |
| Postestival | 10 | 25 | 36 | — | — | — | — |
| Serotinal | 3 | 17 | 21 | 20 | — | — | — |
| Autumnal | 1 | 10 | 23 | 17 | 21 | — | — |
| Hibernal | 0 | 12 | 16 | 25 | 33 | 14 | — |

¹ Refers to mature rats only (see appendix).

These characters are only approximations and for this paper the best that can be done is to state that male rats weighing more than 175 gms. and female rats weighing more than 150 gms. are adults.

SURVIVAL OF RATS

Ia. *Averaged survival of all rats*

During the experiment 1036 rats were marked and released and, in addition, 87 rats were marked and released during the last (hibernal) season. The totals of table III were divided by the number of seasons of observations to get an averaged figure for calculated survival of rats. The cal-

culated survival on the basis of releasing 100 rats is given in table III and the curve is shown by crosses in figure 5. In figure 6 the data for the averaged total are plotted on semilogarithm paper. It will be noted that the rate of survival is constant (straight line) until the fourth season after marking and then sharply decreases.

In obtaining the averaged total survival the figures were not weighted to compensate for differences in numbers of rats caught in the various seasons. This correction can be made by averaging the percentage survival for all the seasons

TABLE III. *Survival of rats on Maryland farm*

| Season of marking | Released | Rats | Survivors from: | | | | | |
|-------------------|----------|------------------|-------------------|--------------------|--------------------|--------------------|--------------------|--------------------|
| | | | 1 season previous | 2 seasons previous | 3 seasons previous | 4 seasons previous | 5 seasons previous | 6 seasons previous |
| Prevernal | 130 | — | — | — | — | — | — | — |
| Vernal | 269 | Recaptured | 29 | — | — | — | — | — |
| | | Not captured | 99 | — | — | — | — | — |
| | | Survivors | 128 | — | — | — | — | — |
| | | Percentage | 98.5 | — | — | — | — | — |
| Estival | 242 | Recaptured | 52 | 16 | — | — | — | — |
| | | Not captured | 130 | 40 | — | — | — | — |
| | | Survivors | 182 | 56 | — | — | — | — |
| | | Percentage | 67.6 | 43.0 | — | — | — | — |
| Postestival | 170 | Recaptured | 36 | 25 | 10 | — | — | — |
| | | Not captured | 130 | 90 | 36 | — | — | — |
| | | Survivors | 166 | 115 | 46 | — | — | — |
| | | Percentage | 68.5 | 42.6 | 36.4 | — | — | — |
| Serotinal | 151 | Recaptured | 20 | 21 | 17 | 3 | — | — |
| | | Not captured | 96 | 100 | 81 | 16 | — | — |
| | | Survivors | 116 | 121 | 98 | 19 | — | — |
| | | Percentage | 68.2 | 50.0 | 36.4 | 14.6 | — | — |
| Autumnal | 74 | Recaptured | 21 | 17 | 23 | 10 | 1 | — |
| | | Not captured | 96 | 78 | 105 | 46 | 4 | — |
| | | Survivors | 117 | 95 | 128 | 56 | 5 | — |
| | | Percentage | 77.5 | 55.9 | 54.8 | 20.8 | 3.9 | — |
| Hibernal | — | Recaptured | 14 | 33 | 25 | 16 | 12 | 0 |
| | | Not captured | 40 | 96 | 73 | 46 | 35 | 0 |
| | | Survivors | 54 | 129 | 98 | 62 | 47 | 0 |
| | | Percentage | 74.0 | 85.2 | 57.7 | 25.6 | 17.4 | 0 |
| Totals | 1036 | Recaptured | 172 | 112 | 75 | 29 | 13 | 0 |
| | | Not captured | 591 | 404 | 295 | 108 | 39 | 0 |
| | | Survivors | 763 | 516 | 370 | 137 | 52 | 0 |
| | | Percentage | 73.6 | 59.9 | 53.6 | 26.5 | 15.1 | 0 |
| | | Average | 127.2 | 103.3 | 92.5 | 45.7 | 26.0 | — |
| | | Weighted average | 64.6 | 54.7 | 45.8 | 20.3 | 10.5 | — |

from table III. This weighted average is not shown in figure 6 and has slightly lower values for each season.

Ib. Survival of rats marked in prevernal season

The survival of rats marked in this season was surprisingly high (table III, figures 5 and 6) for one season and then decreased rapidly (read table III diagonally). The difference between the survival from prevernal to vernal season (98%) and survival of all rats from the first season to the second season (73.6%) is statistically significant. Although the explanation of this high survival is not clear, it may be noted that the rats marked in the prevernal season were mostly adults (71%) whereas in the total population during the year only 51% were adults.

Ic. Survival of rats marked in vernal, estival and postestival seasons

Rats released in these seasons had very similar survival rates (table III, figures 5 and 6). Straight lines drawn through the points plotted on semilogarithm paper (figure 6, dotted lines) are similar but it should be noted that the lines differ in slope in a manner which suggests that the greater the average age of a population, the greater the rate of mortality. The age composition of rats was the same (48-52% adult) in these 3 seasons when the rats were marked but the rats from the vernal season of course were older (about 4 months) than the rats from the

postestival season when observations ended. The downward slope of the curve representing survival of rats marked in the vernal season is greater than the slope of the curve for estival and postestival rats and appears to indicate that older rats have greater mortality.

II. Rats found dead

A second viewpoint of study of the survival of rats is a consideration of the actual length of life of rats found dead. During the year 60 rats were found which had been killed by predators or by accidents (drowning, etc.). For analysis the length of life after marking in terms of seasons was calculated (table IV). For example a rat marked in the vernal season and found dead in the serotinal season was known to live for 3 seasons after marking. In table IV this rat would be one of the 20 known to be alive the third season after marking but known to be dead in the fourth season. To pursue the example further 20 rats were known to be alive in the third season after marking and 11 of them were found dead during that third season, thereby leaving 9 rats known to be alive in the fourth season after marking. For comparison with other survival figures the data for dead rats are calculated in percentages.

The data in table IV and the curve in figure 6 show that the survival rate of this group of rats is very similar to that of total rats but may diverge somewhat in seasons IV, V, and VI.

TABLE IV. *Mortality and disappearance*

| Season after marking | Found dead | Disappearance of rats | | | |
|----------------------|------------|-----------------------|-------------|---------------|---------------|
| | | Adult males | Young males | Adult females | Young females |
| 0 | 60(100) | 115(100) | 105(100) | 134(100) | 119(100) |
| 1 | 44 (73) | 73 (62) | 71 (67) | 101 (75) | 91 (76) |
| 2 | 33 (55) | 42 (37) | 50 (48) | 70 (52) | 59 (50) |
| 3 | 20 (33) | 26 (23) | 32 (30) | 38 (28) | 25 (21) |
| 4 | 9 (15) | 6 (5) | 14 (12) | 15 (11) | 9 (7) |
| 5 | 4 (7) | 3 (2) | 4 (3) | 8 (6) | 1 (1) |
| 6 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 |
| 5% Time | 6.4 | 5.0 | 5.6 | 6.2 | 5.1 |

III. *Survival of rats by age and sex*

It is of course important to compare the survival of the various age and sex categories. It is generally possible to calculate these survivals by the method used to calculate total survival since the weight of the rats (adult or young) is known and the number of rats of the various categories in the whole population can be calculated from the weight ratios of the rats trapped. However, the method is not possible with these data because the small number of recaptured rats in each category causes the calculated survival totals to vary tremendously.

Nevertheless the survival of the various age and sex groups can be compared by considering the disappearance of recaptured rats. This amounts to the observed life of the rats and of course the rats lived for a while after the last capture. The number of survivors in a season is the sum of rats recaptured plus rats not captured but known to be alive because they were captured in a later season but there are in addition some rats which were alive and never recaptured. For example (table IV), 115 adult male rats were recaptured during the experiment and 42 were recaptured the first season after release (season 1) but never caught again, thus leaving 73 survivors, that is, rats caught in some subsequent season. Similarly 31 adult male rats were caught the second season after release (season 2) but never caught again, leaving 42 survivors. Corresponding calculations were made for all ages and sexes. Since the rats were known to be alive when released it is natural that these survival curves should have steeper slopes (figure 6) than the true survival curve of rats found dead.

If it is assumed that the survival after last capture is the same for the various age and sex groups these disappearance data can be used to compare survival rates of the various categories.

From table IV and figure 6 the adult males appear to have a lower survival rate than the other groups. The young females

survived about the same as the adult females until season IV when there was a sharp decline which corresponds roughly to the first or second pregnancy. The low survival might be caused by mortality in connection with reproduction.

IV. *Survival of individual rats*

It will be remembered that at the end of the experiment the rats were caught in steel traps and killed. Hence no rat thus caught could have a record of more than a year and actually no rat marked in the pre-vernal season was trapped in the following hibernal season. However 42 rats, marked in the vernal season, were captured and killed at the end of the hibernal season. Only 4 (2 males, 2 females) of these had lived for 46 weeks. The 2 females were nearly adult when marked and hence were about 20 weeks old (Davis and Winsor, '48). These rats, therefore, lived for about 66 weeks (15 months) because they were probably born about December 1945 and were killed in March 1947.

Since of course not all rats were captured with steel traps at the end of the experiment, trapping was continued at monthly intervals and a few marked rats were caught. Most of these had been recently marked but 1 female was marked on May 14, 1946 (weighed 244 gms.), and was caught May 27, 1947, and has the longest known life of any rat in these studies. Since she was about 18 weeks old when first caught, she lived for about 70 weeks. These longevity records agree well with the calculations because extrapolation of the curve (figure 6) for dead rats indicates that 1 out of 100 rats should be alive 72 weeks after marking. Extrapolation of the curve for total rats indicates that 1 out of 100 rats should be alive 76 weeks after marking.

DISCUSSION

The survival of animals has commonly been indicated by the "turnover period" (Leopold *et al.*, '43; Buss, '46; others), which is defined as the length of time

required for any age class to vanish completely. The fact that 100% of a class must disappear may make the turnover period dependent upon a few long-lived individuals or upon trapping efficiency. From the population viewpoint it is important to know when an age class ceases to be significant in the entire population. It is therefore proposed that the "X per cent survival time" be used where X is a percentage which is considered of negligible importance in the entire population. The percentage selected may vary from species to species or even from place to place or year to year, depending upon conditions and purposes of the work. For many species it seems that "5% survival time" will be satisfactory because in a stable population by the time there are only 5 out of the original 100 left, this age group probably would be of no importance since there would be 95 other individuals from other age groups.

The "X% survival time" also makes possible a comparison of survival curves by smoothing and extrapolation. The 5% survival time for all rats (averaged total) was 7.8 seasons; for rats marked in the prevernal season, 5.8 seasons, for rats marked in the vernal, 9.0 seasons, for rats marked on the estival, 10.6 seasons, for rats marked in the postestival, 12.9 seasons. Table IV shows the 5% survival time for the various groups of rats expressed in biological seasons. The differences in the various categories are at once strikingly evident. In order to get some idea of the variability of the 5% survival time caused by sampling error a test was made with the data for the disappearance of adult females. The rats were divided at random into 2 groups (67 each) and the curves plotted as in figure 6. The 5% time was 6.1 seasons for 1 group and 6.3 seasons for the other. This suggests that the variability due to sampling is of the order of a few tenths of a per cent. Therefore it is likely that the survival of adult females is really greater than the survival of adult males since the 5% survival times differ by 1.2%.

The survival of rats on this farm is based upon recaptured rats and of course is subject to errors due to sampling, estimating of populations and efficiency of the trapping. The calculated survivals however are confirmed by the independent data for the known lives of rats.

Since these data indicate that few rats live more than a year it is worthwhile to consider the implications of this short life. If rats had a short breeding season, say, 1 month, and if 100 rats were alive in March, then by the next March there would be only 4 or 5 of these rats left (figure 6). Such a population of course would soon vanish, but the rats breed throughout the year and thus new individuals appear at all times. However it is likely that in more northern localities, the rats living outdoors breed for only part of the year and thus lack regular replacements in contrast to rats living indoors which apparently breed more regularly and have regular replacements. Actually the long breeding season is extremely important in rat populations by insuring constant replacements. Similar conditions have been found for other rodents (Hamilton, '41; Hacker and Pearson, '44; Davis, '47).

One other point requires notice. In table III it was found that rats released in the prevernal season survived well for 1 season and then survived very poorly. At this season there were few young rats (30% of population) and thus it is concluded that most of the rats were mature at that time. In the vernal and estival seasons the survival was more regular and did not show a sharp change of slope (figure 6). Since in these seasons 50% of the rats were young, it is concluded that the average age of the rats marked in the vernal and estival seasons was less than the age of rats marked in the prevernal season. It is likely that this change of slope of the prevernal rats represents a kind of senility of old rats being reflected in increased mortality. Although there is no reproductive senility, it is possible that

in rats of this age senility is expressed by sluggishness, poor teeth, etc.

Another explanation of the changes in slope is possible. In July a number of sick rats appeared in the traps and some were found dead. A diarrhea and general debility were evident. Although only 2 rats were examined bacteriologically, both had an infection of *Salmonella typhimurium*. Unfortunately the epidemic could not be studied but it might account for the increased mortality at this time.

It can be noted from table I that the population increased and then declined until in March 1947 the population was the same as the preceding March 1946. Although this decrease may have been seasonal, it probably was due to the exhaustion of the corn supply in the crib in June 1946 because the decline continued until the population was less than 100 rats in March 1948. While it is possible that rats in this declining population had a shorter survival time than rats in a stable population, examination of sex and age composition at the various seasons shows no suggestive changes.

SUMMARY

In order to determine how long Brown Rats (*Rattus norvegicus*) live under natural conditions, rats were marked, released and recaptured at later dates on a horse farm near Baltimore, Maryland from March 1946 to March 1947. A total of 1036 rats were marked for this purpose and 366 were recaptured at a later season. For purposes of analysis the year was divided into 7 biological seasons of about 2 months according to temperature and precipitation conditions.

The population in the seasons was calculated by Jackson's ('39) method and the survival of rats estimated by assuming that the ratio of recaptured rats to total rats captured was the same in the untrapped residue as in the trapped sample.

The results indicated that about 5% of the rats live for 1 year. The survival by seasons starting in early spring with 100 rats was: spring 74; summer 60; late summer 54; early fall 27; late fall 15; winter 5 (extrapolation).

The survival of 60 rats which were found dead after marking was essentially the same as above. Adult female rats lived longer than adult male rats.

| | Seasons | | | | | | |
|--|-----------|--------|---------|----------|--------|------|--------|
| | Prevernal | Vernal | Estival | Postest. | Serot. | Aut. | Hiber. |
| Total rats caught | 130 | 298 | 310 | 246 | 212 | 146 | 179 |
| Young rats caught | 21 | 38 | 57 | 49 | 57 | 5 | 28 |
| Mature rats caught (marked and unmarked) | 109 | 260 | 253 | 197 | 155 | 141 | 151 |
| Rats marked (adults and young) | 130 | 269 | 242 | 170 | 151 | 74 | 87 |
| Rats recaptured | 0 | 29 | 68 | 76 | 61 | 72 | 92 |
| Recaptured from prevernal | — | 29 | 16 | 10 | 3 | 1 | 0 |
| Recaptured from vernal | — | — | 52 | 25 | 17 | 10 | 12 |
| Recaptured from estival | — | — | — | 36 | 21 | 23 | 16 |
| Recaptured from postestival | — | — | — | — | 20 | 17 | 25 |
| Recaptured from serotinal | — | — | — | — | — | 21 | 33 |
| Recaptured from autumnal | — | — | — | — | — | — | 14 |

APPENDIX

For the reader who may wish to calculate the population or use the data for other purposes this appendix gives the figures necessary for using Jackson's method ('39).

One point requires emphasis. Very young rats which were not large enough to be marked in a previous season must be subtracted from the total captures. The very young rats (less than 75 gms.) thus subtracted are listed in line 2. These very young rats however should naturally be included in the totals of rats marked and released. Thus mature rats caught (line 3) equals rats marked (line 4) plus rats recaptured (line 5) less very young rats (line 2). If the number of very young rats was negligible or a constant proportion this correction could be ignored but, due to the breeding maxima in May and September, the very young rats must be considered. The population estimate therefore does not include the very young rats born since the previous marking period, and is somewhat lower than the true population, being actually the number of *weaned* rats.

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GRASSLAND TYPES OF SOUTH CENTRAL MONTANA

JOHN C. WRIGHT AND ELNORA A. WRIGHT

Franz Theodore Stone Laboratory, Put-in-Bay, Ohio

INTRODUCTION

The grassland vegetation of south central Montana is of considerable ecological interest, because it lies in the tension zone between the bunch grass prairies of the northwest and the short grass prairie of the great plains. These two grassland types alternate and intermingle along a wide zone of contact as a result of variations in soil and climate induced by the rough and broken topography of this area.

The character of the vegetation over large areas has been greatly changed as a result of overgrazing and cultivation, and in many cases the original nature of the climax can be found only in a few relict areas. The purpose of this study was to locate such areas and to analyze the vegetation occurring thereon. The location of the areas studied is shown on the map (fig. 1). In some cases, a comparison was made between the relict area and pastured land in the same locality, and vegetation differences resulting from grazing were noted. The studies here re-

ported were made in the period from May to August in 1947, while the authors were in residence at Montana State College.

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The plant communities of the unfor-ested regions of Montana have been little studied, and most of the observations are recorded as mere descriptions. Beal (1887) quotes Scribner as saying: "*Poa tenuifolia* (*Poa secunda*) may well be regarded as the grass of the country." However, Lommanasson ('39) points out that this species spreads as a result of drought. Spragg ('02) recognized the changes being wrought by overgrazing and stated that blue grama was the most abundant grass on the prairie benches, whereas before, the Poas, blue joint

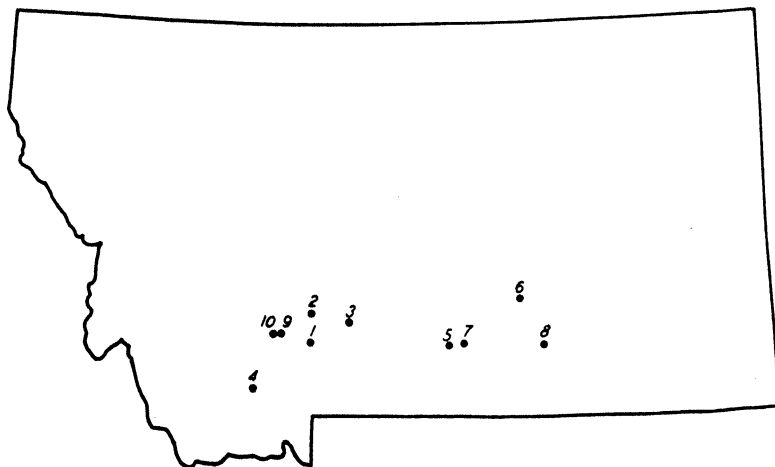


FIG. 1. Map of Montana showing the location of the test areas studied: 1 Bozeman, 2 Gallop, 3 Rock Creek, 4 Virginia City, 5 Square Butte, 6 Pompey's Pillar, 7 Laurel, 8 Hardin, 9 Logan, 10 Three Forks.

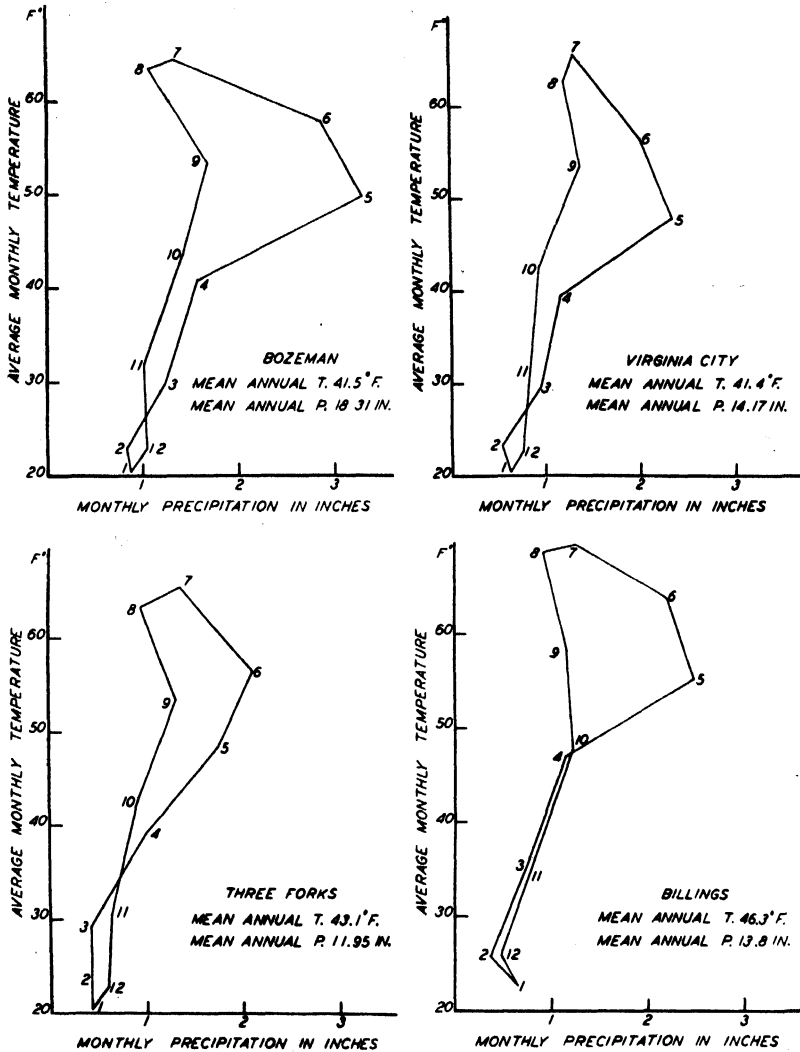


FIG. 2. Climographs for stations typical of the various grassland types.

(*Agropyron smithii*), prairie junegrass (*Koeleria cristata*), and other grasses formed the greater part of the forage. Leiberg ('04) mentions the decline in grazing value of land in this area as a result of overgrazing.

Reitz and Morris ('39) divided the range country of Montana into plains region, central mountain, and western region, and listed the important grasses of each. Morris ('46) classified Montana grasslands on the basis of soils, climate, and grazing.

CLIMATE

Within the normal limits of the prevailing climate of this region, precipitation is generally the factor exerting the major influence on composition, yield, and density of the native range vegetation. The annual precipitation varies from 11.95 inches at Three Forks to 18.03 inches at Bozeman, 68 to 72% of which falls in the period from April 1 to September 30, inclusive.

Temperatures of 100° F. or higher may occur in any month from May to Septem-

ber, and of zero or lower in any month from September to May. Average annual temperature range from 41.9° F. at Bozeman to 46.7° F. at Billings.

In order to correlate the distribution of grassland types with climate, climographs (fig. 2) were prepared from temperature and precipitation data of weather stations typical of the areas studied. The climograph for Bozeman represents areas 1, 2, and 3 (fig. 1); Virginia City, area 4; Billings, areas 5, 6, 7, and 8; and Three Forks, areas 9 and 10. Bozeman, Virginia City, and Three Forks are located in the intermountain region of Montana; whereas Billings lies in the great plains.

Evaporation data are available for only two stations in this region, the Agricultural College at Bozeman and the Huntley Branch Station at Huntley. The precipitation-evaporation ratio at these stations for the months of April to September is 27.17% and 24.87%, respectively.

The frost-free period varies from 133 days at Billings to 115 days at Bozeman.

METHODS

The vegetation was sampled by the line interception method (Canfield, '42). A 25 foot wire was used as a sampling unit. The number of samples taken depended upon the constancy of composition of the area studied. In most cases, four samp-

ling units were considered sufficient. The basal cover of the grasses and grass-like plants was measured. Forbs and shrubs were listed in each area in their order of abundance. In certain of the areas, list quadrats of 625 sq. ft. were made in order that the forbs and shrubs of the relict area and adjoining pasture land might be compared.

No attempt was made to randomize the sampling units, as it was necessary to avoid disturbed areas such as graves, pocket gopher workings, roads, and ditches in making the observations. The data showing the results of the vegetative analyses of the study areas are given in table I. A tabular comparison of certain of the virgin areas and adjacent grazed areas is shown in table II.

DESCRIPTION OF AREAS STUDIED

Area 1.—Catholic Cemetery, one mile north of Bozeman. This area is located on the level floor of the Gallatin Valley. The soil type is Bozeman silt loam. The dominant grass was *Festuca idahoensis*¹ which formed a practically pure stand, ex-

¹Hitchcock, Manual of the Grasses of the United States (1935), is the authority for the grass names used. Coulter and Nelson, New Manual of Rocky Mountain Botany (1937), was used as authority for the names of non-grass plants.

TABLE I. *Density of grass species for areas studied*
(Values are per cents; T is less than .1%)

| Grass species | Station | | | | | | | | | |
|-----------------------------|-------------------|-------------|--------------------|----------------------------|----------------------|------------------------------|-------------|-------------|------------|----------------------|
| | 1 Boze- man | 2 Gallop | 3 Rock Creek | 4 Vir- ginia City | 5 Square Butte | 6 Pom- pey's Pillar | 7 Hardin | 8 Laurel | 9 Logan | 10 Three Forks |
| <i>Festuca idahoensis</i> | 11.3 | 6.7 | 8.8 | | | | | | | |
| <i>Agropyron spicatum</i> | .4 | .4 | | 8.2 | 3.2 | 2.9 | | | | |
| <i>Koeleria cristata</i> | T | | T | 3.5 | .1 | .2 | 1.4 | 4.7 | | |
| <i>Poa secunda</i> | | | T | .5 | .2 | .3 | .6 | .4 | .2 | 2.2 |
| <i>Stipa comata</i> | | | T | | .3 | 2.5 | .8 | 2.1 | 1.9 | .5 |
| <i>Stipa viridula</i> | T | | | | | | 2.2 | | | |
| <i>Bouteloua gracilis</i> | | | | | 1.6 | 10.0 | 6.6 | 2.2 | 5.0 | 16.5 |
| <i>Carex filifolia</i> | | | | | 3.6 | 3.3 | | | 1.3 | |
| <i>Agropyron smithii</i> | T | | | | | | .5 | .1 | | |
| <i>Oryzopsis hymenoides</i> | | | | | T | | | | .2 | |
| Total density | 11.7 | 7.1 | 8.8 | 12.2 | 9.0 | 19.2 | 12.1 | 9.5 | 8.6 | 19.2 |

TABLE II. The dominants of the virgin areas compared with the dominants of adjacent grazed areas

| Type | Location of area | Dominants of virgin areas | Dominants of grazed areas |
|------|---------------------|--|---|
| 1 | Gallop Cemetery | <i>Festuca idahoensis</i> | <i>Artemesia tridentata</i> <i>Artemesia cana</i> |
| 1 | Rock Creek Cemetery | <i>Festuca idahoensis</i> | <i>Koeleria cristata</i> <i>Poa secunda</i> <i>Agropyron spicatum</i> <i>Chrysothamnus nauseosus</i> <i>Gutierrezia sarothrae</i> <i>Koeleria cristata</i> |
| 2 | Virginia City | <i>Agropyron spicatum</i> <i>Koeleria cristata</i> | <i>Artemesia tridentata</i> <i>Gutierrezia sarothrae</i> <i>Agropyron spicatum</i> <i>Artemesia tridentata</i> <i>Gutierrezia sarothrae</i> |
| 3 | Square Butte | <i>Agropyron spicatum</i> <i>Carex filifolia</i> <i>Bouteloua gracilis</i> | |
| 4 | Laurel Cemetery | <i>Koeleria cristata</i> <i>Stipa comata</i> <i>Bouteloua gracilis</i> | |
| 5 | Logan Cemetery | <i>Bouteloua gracilis</i> <i>Stipa comata</i> | <i>Bouteloua gracilis</i> <i>Chrysothamnus nauseosus</i> <i>Gutierrezia sarothrae</i> |

cept in depressed areas and ditches where moisture conditions were favorable enough to permit *Poa pratensis* to maintain itself. Commonly occurring shrubs and forbs in order of decreasing abundance were: *Artemesia cana*, *Lupinus leucophyllus*, *Astragalus drummondii*, *Artemesia gnaphalodes*, *Achillea millefolium*, *Malvastrum coccineum*, and *Erigeron* spp. Other less commonly occurring species were *Arnica latifolia*, *Cirsium hookerianus*, *Potentilla nuttallii*, *Geranium viscosissimum*, *Zygadenus venenosus*, and *Linum lewisii*.

Area 2.—Gallop Cemetery, 23 miles north of Bozeman. The area lies on a gentle west facing slope at the foot of the Bridger Mountains. The soil type is Bridger gravelly loam. Idaho fescue made up 94% of the total grass cover. Commonly occurring shrubs and forbs in order of decreasing abundance were: *Lupinus leucophyllus*, *Artemesia gnaphalodes*, *Astragalus drummondii*, *Artemesia cana*, *Artemesia tridentata*, *Balsamorhiza sagittata*, *Gaura coccinea*, *Gaillardia pinnatifida*, *Tragopogon pratensis*, *Achillea millefolium*, *Helianthus pumilus*, *Hieracium scouleri*, *Erigeron* spp. A comparison was made between the vegetation inside the cemetery and a pastured area adjacent to the cemetery. The vegetation in the pasture was dominated by a dense stand

of *Artemesia tridentata*. A plot of 625 sq. ft. contained 123 plants of *A. tridentata*, and 30 plants of *Artemesia cana*; while inside the cemetery a similar plot contained only 3 plants of *A. tridentata*, 17 of *A. cana*, and 198 of *Lupinus leucophyllus*. The *Festuca idahoensis* was absent in the pasture and had been replaced by *Bromus japonicus* and a few scattered plants of *Agropyron smithii* and *Achillea millefolium*.

Area 3.—Rock Creek Cemetery, 5 miles east of Clyde Park. This cemetery is located on a flat bench overlooking Rock Creek. The soil texture is gravelly loam. Here again *Festuca idahoensis* was dominant with a density of 8.8%. The dominant forb was *Lupinus leucophyllus*. *Gutierrezia sarothrae* was the dominant shrub and *Tetradymia canescens* occurred occasionally. The vigor of the *Gutierrezia sarothrae* was low and many dead plants were noticed. Other commonly occurring forbs present were *Achillea millefolium*, *Phlox hoodii*, *Sedum stenopetalum*, *Castilleja* sp., and *Erigeron pumilus*.

The vegetation in the pasture adjacent to the cemetery was considerably different. *Festuca idahoensis* had practically disappeared and *Lupinus leucophyllus* was greatly reduced in number. *Erigeron* sp., *Chrysopsis villosus*, *Oxytropis* spp., *Phlox*

hoodii, and *Tragopogon pratensis* were abundant. The density of the grass was 3.1%; its composition was *Koeleria cristata* 40.8%, *Poa secunda* 27.1%, *Agropyron spicatum* 24.1%, *Stipa comata* 6.6%, and *Carex filifolia* 1.5% included, though not a grass.

Pocket gophers (*Thomomys talpoides*) were a disturbing factor in this enclosure as well as in the two preceding study areas. These animals had practically eliminated *Festuca idahoensis* where they were active; and as a result, the annual brome grasses, *Bromus japonicus* and *B. tectorum*, came in along with such weeds as *Tragopogon pratensis*, *Achillea millefolium*, and *Erigeron* sp.

Area 4.—Virginia City Cemetery. The area lies on a gentle west slope on the foothills north of the city. The soil is gravelly loam. *Agropyron spicatum* was dominant, comprising 66.4% of the grass cover. The widely spaced shrubs of the area were *Gutierrezia sarothrae* and *Chrysothamnus nauseosus*. Common forbs were *Astragalus* spp., *Artemisia frigida*, *Malvastrum coccineum*, *Phlox hoodii*, *Achillea millefolium*, *Tragopogon pratensis*,

and a few clumps of *Opuntia polyacantha*.

In the pasture outside the cemetery, *Chrysothamnus nauseosus* and *Gutierrezia sarothrae* were in abundance. *Agropyron spicatum* was present as relicts under the protection of bushes of *Chrysothamnus*. The dominant grass was *Koeleria cristata*, but its vigor was very low, and there were only 1 or 2 fruiting panicles per bunch.

Area 5.—Square Butte, located 6 miles west of Laurel. This study area of about three acres is a small butte rising abruptly from the floor of Yellowstone Valley (fig. 3). The sides of the butte are perpendicular around most of its circumference and are inaccessible to livestock. The soil is Billings sandy loam and is firmly stabilized by a luxuriant cover of native grasses, except on the very edges where wind and water erosion are slowly working into the grassland. The dominant plants were *Carex filifolia*, *Agropyron spicatum*, and *Bouteloua gracilis* (fig. 4). *Stipa comata*, *Poa secunda*, and *Koeleria cristata* were of secondary importance, with *Festuca octoflora* and *Bromus tectorum* occurring occasionally in the spaces



FIG. 3. View of Square Butte (background), and overgrazed bench (foreground) showing abundance of sagebrush (*Artemisia tridentata*) and the relict occurrence of *Agropyron spicatum* within the protection of the sagebrush.

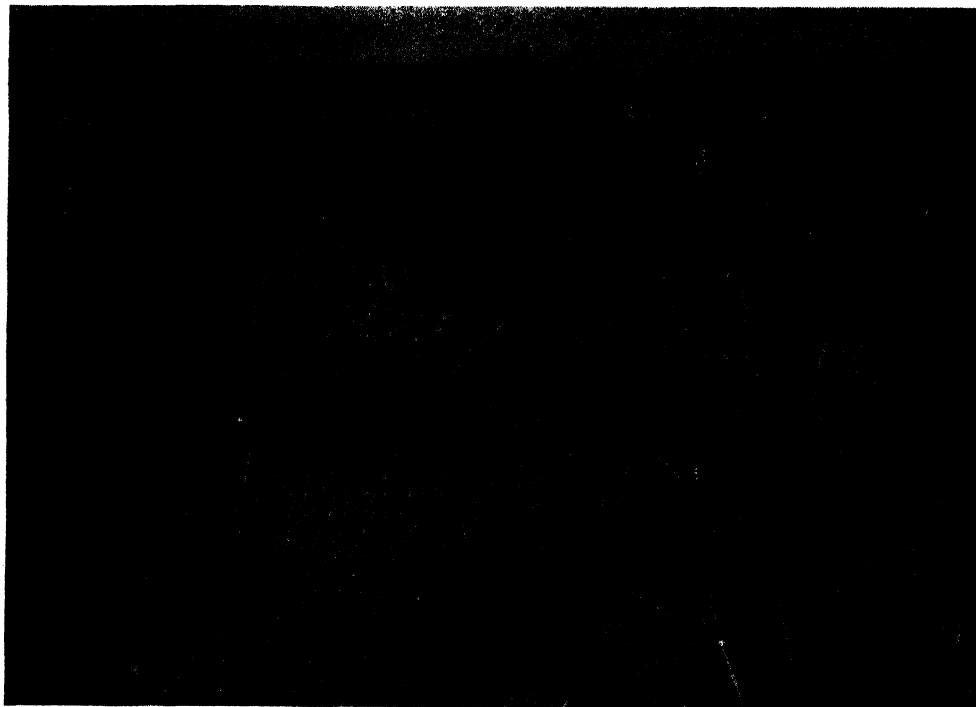


FIG. 4. Climax grassland on top of Square Butte showing the dominance of *Agropyron spicatum* which obscures the lower growing *Carex filifolia* and *Bouteloua gracilis*. Note the absence of *Artemisia tridentata* and the abundance of *Yucca glauca*.

between the bunch grasses. *Artemesia frigida*, *Gutierrezia sarothrae*, *Yucca glauca*, *Astragalus* spp., *Malvastrum coccinimum*, and *Psoralea tenuiflora* were the prominent forbs, and widely scattered bushes of *Chrysothamnus nauseosus* and *Rhus trilobata* were present throughout the area. *Artemesia tridentata* was of infrequent occurrence and confined to the edges of the butte, along with several scraggly trees of *Pinus ponderosa*.

A comparative study was also made of the grazed bench located across the valley and $\frac{1}{4}$ mile to the north of Square Butte. The soil, slope, and elevation of the bench are in general the same as on the butte. It is part of the same geological formation (Eagle Sandstone) from which the butte has become isolated by erosion. The effect of heavy grazing upon the composition of the plant cover of the bench presented a striking contrast (fig. 3).

Artemesia tridentata, which appeared only as a few scattered plants confined to the edges of the butte where the grass density was low, was the dominant plant on the grazed bench. A list quadrat of 625 sq. ft. on the bench contained 108 plants of *A. tridentata*. One of the dominant grasses of the butte, *Agropyron spicatum*, was present here only as relicts protected by the cover of sagebrush plants where stock was unable to graze them down. The other dominants were entirely absent. *Gutierrezia sarothrae* and scattered small bunches of *Kaeleria cristata* and *Poa secunda* occurred between the sagebrush plants.

Area 6.—Pompey's Pillar, located on the south bank of the Yellowstone River, 35 miles east of Billings. The area studied was the north facing slope of the pillar. The soil is sandy loam. This small butte of about $\frac{1}{2}$ acre is a prominent landmark

in the early Montana history. Captain Clark, as quoted by Thwaite ('05), described the butte as a "rock 200 feet high and 400 paces in secumpherance and only axcessable on one side which is the N. E. —on the top there is a tolerable soil of about 5 or 6 feet thick covered with short grass."

A vegetation analysis of the area indicated that *Bouteloua gracilis* made up more than half of the cover, while *Carex filifolia*, *Agropyron spicatum*, and *Stipa comata* were about equally important in making up the rest of the cover.

Artemesia frigida and *Eurotia lanata* were the most abundant shrubs, with *Artemesia dracunculoides*, *A. cana*, *A. tridentata* present only sparingly. Forbs found here were *Petalostemon oligophyllus*, *Psoralea tenuiflora*, *Chrysopsis villosa*, *Yucca glauca*, *Antennaria* sp., and *Gutierrezia sarothrae*.

Along the dry windswept edges, *Ory-*

zopsis hymenoides, *Calamovilfa longifolia*, and *Aristida longiseta* were present, accompanied by scattered shrubs of *Chrysothamnus graveolens*, *Phlox hoodii*, and *Atriplex confertifolia*.

Area 7.—Laurel Cemetery, 1 mile north of Laurel. The area has been fenced since 1909. It lies on the first terrace north of the city, and the soil type is Billings clay loam. The dominant grasses were *Koeleria cristata*, *Bouteloua gracilis*, and *Stipa comata*. *Phlox hoodii*, *Opuntia polyacantha*, *Artemesia frigida*, *Tragopogon pratensis*, *Malvastrum coccinium* were of frequent occurrence. *Artemesia tridentata* occurred only on old graves and was absent entirely on undisturbed portions of the cemetery. On a severely overgrazed pasture 0.2 miles north of the cemetery, 200 plants of *Artemesia tridentata* were counted in a 625 sq. ft. quadrat. *Gutierrezia sarothrae* was abundant, and only widely scattered bunches of *Poa*



FIG. 5. View of cemetery between Logan and Three Forks showing the vigor and abundance of *Stipa comata*.

secunda, *Bouteloua gracilis*, and *Koeleria cristata* were present.

Area 8.—Hardin Cemetery. The Hardin Cemetery lies on a gentle south slope about $\frac{1}{2}$ mile north of the city. The soil type is Cherry silt loam. *Bouteloua gracilis*, *Stipa viridula*, and *Koeleria cristata* were dominant, with *Stipa comata*, *Agropyron smithii*, and *Poa secunda* of secondary importance. *Malvastrum coccineum*, *Phlox hoodii*, *Gutierrezia sarothrae*, and *Opuntia polyacantha* were the common forbs. Occasional plants of *Eurotia lanata* were present. *Bromus japonicus* and *Tragopogon pratensis* were noticed between the bunches of perennial grasses in some areas.

Area 9.—Cemetery between Logan and Three Forks. This is an area located on top of the benchland two miles west of Logan. The soil is coarse and sandy in texture. *Bouteloua gracilis*, *Stipa comata*, and *Carex filifolia* were the dominants (fig. 5). *Oryzopsis hymenoides* and *Poa*

secunda were of secondary importance, although the former was abundant on old graves and cleared areas. *Calamovilfa longifolia* was present in a blow-out spot outside the cemetery.

The density of the grass in the pasture outside the cemetery was 11.5%, as compared to 8.6% inside. This increase in density was due to the increase in abundance of *Bouteloua gracilis* which comprised 89.4% of the vegetation in the pasture in contrast to 58.3% inside the cemetery. *Stipa comata* made up 6.3% of the cover in the pasture as compared to 22.1% inside (fig. 6).

Shrubs and cactus clumps were more abundant in the pasture than in the cemetery. A 625 sq. ft. plot in the cemetery contained 76 plants of *Artemisia frigida*, 11 clumps of *Opuntia polyacantha*, 15 *Chrysothamnus nauseosus*, 12 *Gutierrezia sarothrae* and 1 *Tetradymia canascens*.

Area 10.—Fairview Cemetery, Three Forks. Here, the cemetery lies on a



FIG. 6. Vegetation on pasture outside the cemetery shown in figure 5. *Bouteloua gracilis* is the dominant grass and the invading shrubs are *Gutierrezia sarothrae* and *Chrysothamnus nauseosus*. Note the low vigor of *Stipa comata*.

gradual west facing slope at the foot of a steep hill. The soil type is Manhattan gravelly loam. *Bouteloua gracilis* was the dominant plant, comprising 88.3% of the grass cover. *Poa secunda* was next in abundance, while *Stipa comata* was of little importance.

DISCUSSION

The vegetation of the areas studied in this paper has been classified into 5 types. The types have been named according to the most prominent species in each and are listed as follows, from the most mesophytic to the most xerophytic: (1) *Festuca idahoensis* type, (2) *Agropyron spicatum* type, (3) *Agropyron spicatum*-*Carex filifolia*-*Bouteloua gracilis* type, (4) *Bouteloua gracilis*-*Stipa comata*-*Koeleria cristata* type, and (5) *Bouteloua gracilis*-*Stipa comata* type.

(1) *Festuca idahoensis* type is typified by areas 1, 2, and 3, and occurred in regions of good, well-drained soils and favorable moisture conditions. The climograph (fig. 2) of Bozeman, a typical example of the Idaho fescue type, shows the favorable climatic conditions responsible for its development. The total annual rainfall, 18.31 inches, is the highest of any region studied. The average rainfall for May and June is 3.30 inches and 2.91 inches, respectively. Winter precipitation is higher here than in the other areas, resulting in a more favorable soil moisture balance in the spring which, when coupled with the abundant precipitation received in May and June and relatively cool growing season, accounts for the richer and more varied flora of this region. In no other community studied was the herbaceous vegetation so abundant and varied.

There is a striking resemblance between this grassland type in south central Montana and the Festucetum of Southeastern Washington and adjacent Idaho described by Daubenmire ('42).

The activities of pocket gophers resulting in the influx of subclimax species were noted in each of the three areas. Apparently the destruction of the Idaho fescue

by the pocket gophers was conducive to the invasion of such ruderals as *Tragopogon pratensis*, *Bromus japonicus*, *B. tectorum*, *Achillea millefolium*, *Erigeron* spp., and *Sisymbrium altissimum*.

Some profound changes have occurred in the *Festuca idahoensis* type in south central Montana, as is shown by the absence of native prairie and the predominance of cultivated and pasture land. The rougher portions are used for grazing land; in the moister portions, Idaho fescue has been replaced by *Poa pratensis* and *Phleum pratense*; on deeper, well-drained soils in drier situations, *Artemisia tridentata* has become very prominent; and on shallower, rocky soils, there has been an increase in the abundance of such herbs as *Balsamorhiza sagittata*, *Chrysopsis villosa*, *Lupinus* sp., and *Geranium viscosissimum*.

(2) *Agropyron spicatum* type. Area 4, near Virginia City, belongs to this type. Reference to the climograph of Virginia City (fig. 2) shows the annual precipitation to be 14.17 inches, 4.14 inches less than at Bozeman. Precipitation for May and June is 2.38 inches and 2.05 inches, respectively, as compared to 3.30 inches and 2.91 inches for the same months at the Bozeman station. Winter precipitation, also, is less than at Bozeman resulting in a less favorable soil moisture balance in the spring. However, little difference exists between the average monthly temperatures of the two stations. As the habitat becomes drier, Idaho fescue and its associated forbs drop out, leaving *Agropyron spicatum* dominating the vegetation as it does at Virginia City. On the foothills of the Bridger Mountains the two communities alternate, *Agropyron spicatum* occupying the drier south-facing slopes, while *Festuca idahoensis* is found on the less arid north-facing slopes.

It was noted that under severe grazing, especially by cattle, the *Agropyron spicatum* was eliminated and replaced by species less desirable as forage. Under moderately heavy grazing, *Agropyron spicatum* is replaced by such prairie

grasses as *Stipa comata*, *Koeleria cristata*, and *Poa secunda*. This seems to be an intermediate step between the *Agropyron spicatum* bunch grass stage and the annual grass stage which is characterized by almost pure stands of *Bromus tectorum*.

(3) *Agropyron spicatum*-*Carex filifolia*-*Bouteloua gracilis* type. Area 5, and to a lesser extent Area 6, are classified in this type, which is dependent upon the presence of sandy soil; since on the heavier soils of this region, *Bouteloua gracilis*, *Stipa comata*, and *Koeleria cristata* (Type 4) are dominant.

Weather data from the Billings station (fig. 2) have been selected as typical for these two types. Comparison of the climograph for Billings with those of Virginia City and Bozeman reveals several facts. Winter precipitation is lighter at Billings than at Virginia City and Bozeman; while precipitation during May and June is comparable with that of Virginia City; but it will be noted that the mean annual temperature for Billings is 46.3° F., as compared to 41.4° F. for Virginia City and 41.5° F. at Bozeman. The combination of dry winters and higher temperatures during the spring and early summer, when adequate moisture is available for growth, favors the great plains type of flora at Billings. The compensating factor that allows *Agropyron spicatum* to extend into this region seems to be the presence of sandy soils. The ability of such soils to absorb all of the rain falling on them, and the deep penetration of soil water which their coarse texture allows, provides a source of moisture which this relatively deep-rooted bunch grass can utilize.

This type may be regarded as a transition type between the bunch grass prairies of the intermountain valleys and the mixed grass prairie of the great plains. Much of the land is devoted to dry land farming. The rougher, drier portions are used for grazing. Reference is made here to the study mentioned in Area 5 as an example of how *Artemisia tridentata* increased as a result of severe grazing.

(4) *Bouteloua gracilis*-*Stipa comata*-*Koeleria cristata* type. Areas 7 and 8 appear to have sufficient resemblance, in species and climatic conditions, to be classified as being in this type. The cemetery at Hardin was atypical due to the abundance of *Stipa viridula*; however, the area lies near the base of a long gentle slope, thus receiving additional moisture by runoff from the slope above and possibly from melting snow drifts and seepage which enables *Stipa viridula* to flourish. The climograph for the Billings area is typical of this type (fig. 2).

(5) *Bouteloua gracilis*-*Stipa comata* type. Areas 9 and 10 belong here and are characteristic of the dry western portion of the Gallatin Valley. As can be seen from the climograph for Three Forks (fig. 2), this type is the most xeric of the areas studied.

The total annual rainfall, 11.95 inches, is less than any other station. Precipitation for May and June averages only 1.73 inches and 2.09 inches, respectively. It will be noted that this is the only station where the amount of rainfall received in May is less than that received in June. Consequently, the period of greatest rainfall occurs when temperatures are higher as contrasted to the Virginia City and Bozeman regions which receive the greatest precipitation in May. Thus the great plains flora is favored. The climate is so xeric that sandy soils are not a great enough compensating factor to allow *Agropyron spicatum* to occupy this region as it does in the sandy soils in the Billings area. It will be noted that *Carex filifolia* is fairly abundant in the sandy soils of Area 9 but not present in the denser soils of Area 10. *Koeleria cristata* which formed a considerable proportion of the typical great plains flora represented in types 7 and 8, was absent in both the Three Forks and Logan areas. *Stipa comata* was considerably less abundant on the heavier soils of the Three Forks cemetery than on the sandy soils of the cemetery west of Logan.

The bunch grasses, *Agropyron spicatum*

and *Festuca idahoensis*, reach their maximum development in the Palouse prairie region where precipitation is confined chiefly to the winter months. Growth is possible only in the early spring when the frost free temperatures overlap the moist soil period. In the region of Montana studied, winter precipitation is much lighter and spring and early summer rainfall forms the bulk of the precipitation. However, the cool spring and summer temperatures of the intermountain valleys favor the bunch grasses. In contrast, the short grasses represented in types 3, 4, and 5 are found in regions where the period of maximum rainfall is accompanied by higher temperatures.

There is considerable evidence in certain areas of Utah (Pickford, '32, and Stoddard, '41), southern Idaho (Craddock and Forsling, '38), Idaho and Washington (Humphrey, '45), and British Columbia (Tisdale, '47), that overgrazing has decreased the density and vigor of the desirable grasses and permitted the invasion of sagebrush. The results of the present study in the south central part of Montana seem to indicate that their conclusions apply also in the present study region.

The determination of the extent of sagebrush invasion is an important problem in this part of Montana from the standpoint of the value of brush eradication and range reseeding. As Robertson ('47) points out: "Probably most fruitful for both reseeding and brush eradication will be the extensive but as yet poorly delimited sagebrush ranges lying within the general grassland climate."

SUMMARY

The preceding study presents the results of analyses of the vegetation in ten relict grassland communities in south central Montana. The rough and broken topography of this section results in an alternation and intermingling of the bunch grass prairie extending into the region from the northwest and the short grass prairie of the great plains.

The vegetation of these areas was classified into five types: (1) *Festuca idahoensis* type, (2) *Agropyron spicatum* type, (3) *Agropyron spicatum*-*Carex filifolia*-*Bouteloua gracilis* type, (4) *Bouteloua gracilis*-*Stipa comata*-*Koeleria cristata* type, and (5) *Bouteloua gracilis*-*Stipa comata* type, arranged in order from the most mesophytic to the most xerophytic.

The *Festuca idahoensis* type, the most mesic, occurred in the foothills of the intermountain regions; whereas, *Agropyron spicatum* is dominant in the drier portions. The two communities are favored by the relatively cool growing season of the intermountain region.

The *Agropyron spicatum*-*Carex filifolia* *Bouteloua gracilis* type is transitional between the bunch grass zones of the foothills and the mixed grass prairies of the great plains. The presence of *Agropyron spicatum* here is correlated with sandy soils.

The *Bouteloua gracilis*-*Stipa comata*-*Koeleria cristata* type is a characteristic great plains association and occurs over large areas of eastern Montana. In the drier phases, *Koeleria cristata* drops out.

The increase of sagebrush in parts of the south central region of Montana was discussed. As a direct result of overgrazing the vigor and density of the native grasses have been reduced and the undesirable shrub, *Artemisia tridentata*, allowed to predominate.

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ECOLOGICAL SEGREGATION OF INTER-FERTILE SPECIES OF COLIAS

WILLIAM HOVANITZ

Wayne University, Detroit, Michigan

A test of the ecological isolation of two closely related and inter-fertile species of *Colias* butterflies, *Colias eurytheme* and *Colias philodice*, was made in the states of Ohio, Michigan and Illinois. Samples of the adult butterflies were taken in a number of different localities in order to determine the natural preference of the species where the individuals were observed flying over the same general terrain.

THE METHOD

The method of analyzing the populations consisted of collecting a random sample of the butterflies, male and female, from adjacent or nearby red clover and alfalfa fields without regard to their color characteristics. These samples were made as follows. One series of daily samples was taken one mile south of Ann Arbor, Michigan, in adjacent fields as shown on the accompanying map (figure 1). The number of individuals taken was rather small on any one day but the sampling continued for a week from August 14, 1946, until August 22, 1946. A second sample was taken about two hundred miles to the south in the vicinity of Celina, Ohio, on October 26, 1947. The proportion of the two species in the area was quite different from that in the Ann Arbor area. The two fields analyzed here were not adjacent but were nearby. The third sample test was made about three hundred miles to the west of Ann Arbor in the vicinity of Rockford, Illinois, on Sept. 13, 1947. Again, the relative proportions of the two species in the area were different from those in the other localities. The accompanying map (figure 1) shows the general positions of the three localities.

Colias philodice and *Colias eurytheme* may generally be distinguished from one another by a suffusion of orange pigment

which covers the upper side of the fore wings of the latter and which is absent on the wings of the former. There are other characteristics, too, which may be used on a quantitative basis. One of these is a border-band difference which will be described in more detail in a later publication. The well-known white female form of each of these species occurs in these populations. In the latter individuals it is not possible to distinguish the species by the orange pigment and therefore other characteristics have had to be used. Hybridization and the production of intermediates in the populations also has made it difficult at times to be sure of the species identification of the white females. Nevertheless, the identifications have not often been in error as shown by a close resemblance in the frequency of intermediates determined in the white females as compared to those found in the orange individuals.

The intermediates which are mentioned in this paper refer to individuals which show the following characteristics. In the orange or yellow males and females, the intermediates are those which fit the graded series of ten (Hovanitz, '44) from Grade 2 through Grade 8 in the males and through Grade 7 in the females. In the females, the intermediates are judged by a number of characteristics dealing with the black border band width, size and distribution of the spots inside the band and the intensity of the orange pigment in the hind wing cell spot.

The results of the sampling show a statistical difference in the proportions of the two species and intermediates between them in the alfalfa and red clover fields in each of the three locations studied. These data are given in tables I through VI.

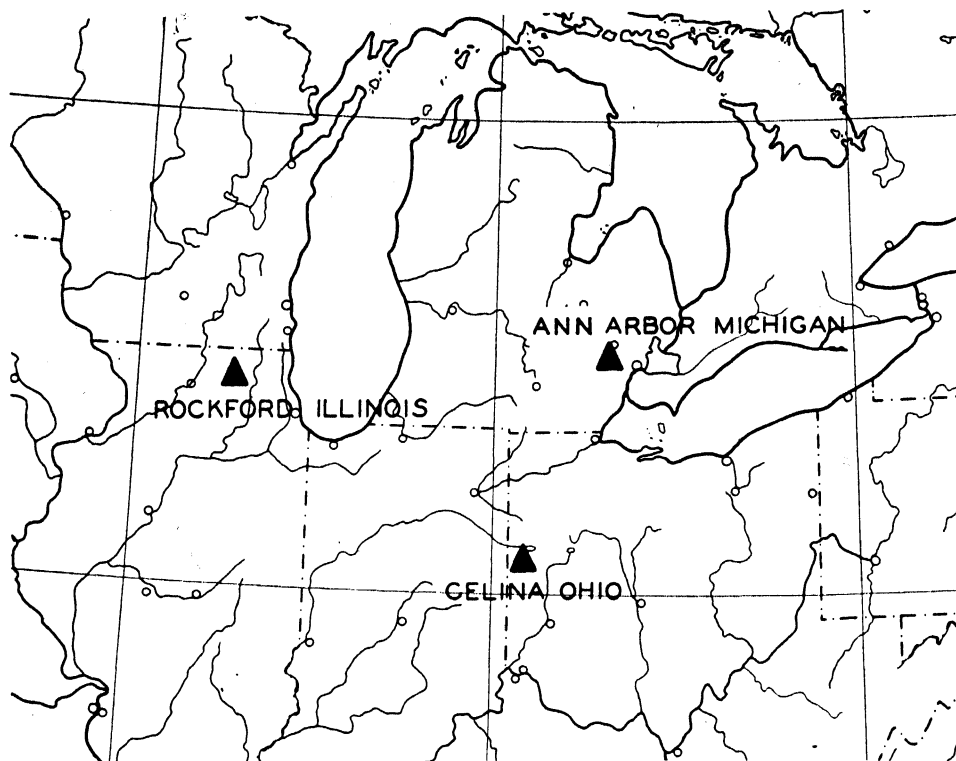


FIG. 1. Map showing the locations of the three population areas in the southern Great Lakes region which have been analyzed in this study.

In these tables, the frequencies of a species or the intermediates are given as the percentage of the total *Colias* butterflies of that sex caught in the field. The standard error of the percentage was then calculated for each by means of the formula

$$\sqrt{\frac{p \cdot q}{n}},$$

where p equals the fraction of the class considered and q equals the fraction of the remaining two classes ($1 - p$).

The total number of butterflies at a location was obtained by summing the data for the two fields at each locality. The significance of the difference between the red clover and alfalfa field samples was tested by assuming that they are not different and that the sum of the two fields most nearly represents the true value for the fields (the null hypothesis). The dif-

ference in the percentage is given for each field as well as the standard error of the difference as computed by the formula

$$t = \frac{p_1 - p_2}{\sqrt{PQ \left(\frac{1}{N_1} + \frac{1}{N_2} \right)}}$$

where P equals the population fraction and Q equals $1 - P$. Here,

$$P = \frac{N_1 p_1 + N_2 p_2}{N_1 + N_2}$$

and p_1 equals the fraction in the alfalfa field, p_2 the fraction in the clover field.

THE RESULTS

The fields at Ann Arbor show a difference between the red clover and alfalfa fields in the direction of higher *eurytheme* (orange) male frequency in the alfalfa than in the red clover field and of higher

TABLE I. *The frequency of C. eurytheme (orange) males in Ann Arbor, Michigan, adjacent alfalfa and red clover fields as compared with the total C. eurytheme, C. philodice (yellow) males and intermediates between them*

| | Clover % | S.E. | N. | Alfalfa % | S.E. | N. | Location total % | S.E. | N. | Difference % | t | Probability | High freq. in field |
|------------------|----------|--------|-----|-----------|--------|----|------------------|-------|-----|--------------|------|-------------|---------------------|
| Aug. 14, 1946 | 23.81 | ± 9.29 | 21 | 33.33 | ±11.11 | 18 | 28.21 | ±7.21 | 39 | 9.52 | .66 | >.05 | alfalfa |
| Aug. 15, 1946 | 20.00 | ±10.33 | 15 | 42.86 | ±18.70 | 7 | 27.27 | ±9.49 | 22 | 22.86 | 1.12 | >.05 | alfalfa |
| Aug. 16, 1946 | 18.18 | ± 6.71 | 33 | 50.00 | ± 9.81 | 26 | 32.20 | ±6.08 | 59 | 31.82 | 2.60 | <.01 | alfalfa |
| Aug. 19, 1946 | 15.38 | ± 7.08 | 26 | 35.29 | ±11.59 | 17 | 23.26 | ±6.44 | 43 | 19.91 | 1.51 | >.05 | alfalfa |
| Aug. 21, 1946 | 21.05 | ± 6.61 | 38 | 27.78 | ± 7.47 | 36 | 24.32 | ±4.99 | 74 | 6.73 | 0.67 | >.05 | alfalfa |
| Aug. 22, 1946 | 32.06 | ± 8.38 | 31 | 0.00 | — | 17 | 20.83 | ±5.86 | 48 | 32.06 | 2.62 | <.01 | clover |
| Total Aug. 14-19 | 18.95 | ± 3.77 | 108 | 41.18 | ± 5.40 | 83 | 28.22 | ±3.26 | 191 | 22.23 | 3.38 | <.01 | alfalfa |
| Total Aug. 21-22 | 26.09 | ± 4.58 | 92 | 18.87 | ± 4.97 | 62 | 22.95 | ±3.39 | 154 | 7.22 | 1.04 | >.05 | clover |

philodice (yellow) male frequency in the clover field than in the alfalfa field on each of the six days during which tests were made except Aug. 22 (table I). The differences were greatest in the period Aug. 14 until Aug. 19 and then dropped on Aug. 21. On Aug. 22 the direction of the difference had changed so that the proportion of yellow was now higher in the alfalfa field than in the clover field. There were in fact no *eurytheme* taken at all in the alfalfa field on Aug. 22.

The test of significance indicates that the only two daily samples taken which are significantly different at less than the 5% level are those on Aug. 16 and Aug. 22. These are different in opposite directions as may be seen by reference to table I.

Since the physical characteristics of the fields were changed in the period Aug. 20-22 by the cutting of the alfalfa field by the farmer, totals for the fields were obtained for the period before the cutting when the fields were left in an un-

molested condition (Aug. 14-19) and the period during and after the cutting (Aug. 21-22). The alfalfa field was one half cut on Aug. 21 and completely cut on Aug. 22. The clover field, however, was continuously in an unmolested condition.

For the first period, the orange *eurytheme* was relatively more common in the alfalfa field than in the clover field as indicated by the difference $22.23 \pm 6.57\%$. There was no good way of determining the absolute abundance of this species in the two fields at the time and whether or not there was an absolute difference is not known. During the same period, the yellow *philodice* males were relatively more abundant in the clover field as shown by the difference $22.43 \pm 6.84\%$ (table II). Again there is no good way of determining the absolute abundance of the species in the two fields. No differences in the distribution of the intermediates in the fields is indicated by the data (table III).

During the second period, Aug. 21-22, the frequencies were reversed. The

TABLE II. *The frequency of C. philodice (yellow) males in Ann Arbor, Michigan, adjacent alfalfa and red clover fields as compared with the total C. philodice, C. eurytheme (orange) males and intermediates between them*

| | Clover % | S.E. | N. | Alfalfa % | S.E. | N. | Location total % | S.E. | N. | Difference % | t | Probability | High freq. in field |
|------------------|----------|--------|-----|-----------|--------|----|------------------|-------|-----|--------------|------|-------------|---------------------|
| Aug. 14, 1946 | 76.19 | ± 9.29 | 21 | 66.67 | ±11.11 | 18 | 71.79 | ±7.21 | 39 | 9.52 | 0.66 | >.05 | clover |
| Aug. 15, 1946 | 73.33 | ±11.42 | 15 | 57.14 | ±18.70 | 7 | 68.18 | ±9.93 | 22 | 16.19 | 0.76 | >.05 | clover |
| Aug. 16, 1946 | 78.79 | ± 7.12 | 33 | 46.15 | ± 9.78 | 26 | 64.41 | ±6.23 | 59 | 32.64 | 2.60 | <.01 | clover |
| Aug. 19, 1946 | 76.92 | ± 8.26 | 26 | 52.94 | ±12.11 | 17 | 67.44 | ±7.15 | 43 | 23.98 | 1.64 | >.05 | clover |
| Aug. 21, 1946 | 73.68 | ± 7.14 | 38 | 69.44 | ± 7.68 | 36 | 71.62 | ±5.24 | 74 | 4.24 | 0.40 | >.05 | clover |
| Aug. 22, 1946 | 64.52 | ± 8.59 | 31 | 88.24 | ± 7.81 | 17 | 72.92 | ±6.41 | 48 | 23.72 | 1.77 | >.05 | alfalfa |
| Total Aug. 14-19 | 76.84 | ± 4.06 | 108 | 54.41 | ± 5.47 | 83 | 67.48 | ±3.39 | 191 | 22.43 | 3.28 | <.01 | clover |
| Total Aug. 21-22 | 69.57 | ± 4.80 | 92 | 75.47 | ± 5.46 | 62 | 72.13 | ±3.61 | 154 | 5.90 | 0.80 | >.05 | alfalfa |

TABLE III. *The frequency of C. philodice-eurytheme intermediate males in Ann Arbor, Michigan, adjacent alfalfa and red clover fields, as compared with the total intermediate and typical forms of both species*

| | Clover % | S.E. | N. | Alfalfa % | S.E. | N. | Location total % | S.E. | N. | Difference % | t | Probability |
|------------------|----------|-------|-----|-----------|-------|----|------------------|-------|-----|--------------|------|-------------|
| Aug. 14, 1946 | 0.00 | — | 21 | 0.00 | — | 18 | 0.00 | — | 39 | 0.00 | — | — |
| Aug. 15, 1946 | 6.67 | ±6.44 | 15 | 0.00 | — | 7 | 4.55 | ±4.44 | 22 | 6.67 | 0.70 | >.05 |
| Aug. 16, 1946 | 3.03 | ±2.98 | 33 | 3.85 | ±3.77 | 26 | 3.39 | ±2.36 | 59 | 0.82 | 0.17 | >.05 |
| Aug. 19, 1946 | 7.69 | ±5.23 | 26 | 11.76 | ±7.81 | 17 | 9.30 | ±4.43 | 43 | 4.07 | 0.45 | >.05 |
| Aug. 21, 1946 | 5.26 | ±3.62 | 38 | 2.78 | ±2.74 | 36 | 4.05 | ±2.29 | 74 | 2.48 | 0.54 | >.05 |
| Aug. 22, 1946 | 3.23 | ±3.18 | 31 | 11.76 | ±7.81 | 17 | 6.25 | ±3.49 | 48 | 8.53 | 1.17 | >.05 |
| Total Aug. 14-19 | 4.21 | ±1.93 | 108 | 4.41 | ±2.25 | 83 | 4.29 | ±1.47 | 191 | 0.20 | 0.07 | >.05 |
| Total Aug. 21-22 | 4.35 | ±2.13 | 92 | 5.66 | ±2.93 | 62 | 4.92 | ±1.74 | 154 | 1.31 | 0.37 | >.05 |

orange *eurytheme* was more common in the clover fields than in the alfalfa, and the yellow *philodice* was comparatively more common in the alfalfa than in the clover field. Again there was no difference in the intermediates. There was a noticeable scarcity of butterflies at the time of the cutting of the alfalfa field.

The number of female butterflies in the fields during the period of the sampling was much smaller than that of the males and the daily samples were relatively small. The data were therefore lumped to form totals for the two periods as given above. These data are given in table IV. The orange *eurytheme* was still more abundant in the alfalfa field and the yellow *philodice* in the clover field during the period Aug. 14-19 and reversed during the second period Aug. 21-22, but in no case are the differences between the two fields significant at less than the 5% level. In the case of the

intermediate females during the first period there are more intermediates in the clover field than in the alfalfa field and the difference $23.08 \pm 11.72\%$ is significant at about the 5% level.

Only one sample each was made in the clover and alfalfa fields in the vicinity of Rockford, Illinois, and Celina, Ohio. The data for Rockford, Illinois, are given in table V and those for Celina, Ohio, are given in table VI.

The difference in the relative proportions of the two species in the red clover and alfalfa fields at Rockford, Illinois, is in the same direction as indicated for Ann Arbor, Michigan. The males of the orange *eurytheme* were comparatively more abundant in the alfalfa field than in the clover field as shown by the difference $70.41 \pm 11.11\%$. The males of yellow *philodice* were comparatively more abundant in the red clover field than in the alfalfa field as shown by the difference

TABLE IV. *The female frequency of Colias philodice (yellow), Colias eurytheme (orange) and intermediates between them in Ann Arbor, Michigan, adjacent alfalfa and red clover fields. Percentage of total*

| | Clover % | S.E. | N. | Alfalfa % | S.E. | N. | Location total % | S.E. | N. | Difference % | t | Probability | High freq. in field |
|------------------------|----------|--------|----|-----------|--------|----|------------------|-------|----|--------------|------|-------------|---------------------|
| <i>philodice</i> : | | | | | | | | | | | | | |
| Aug. 14-19 | 69.23 | ±12.80 | 13 | 66.67 | ±12.17 | 15 | 67.86 | ±8.83 | 28 | 2.56 | 0.14 | >.05 | clover |
| Aug. 21-22 | 82.61 | ± 7.90 | 23 | 100.00 | 0.00 | 9 | 87.50 | ±5.85 | 32 | 17.39 | 1.34 | >.05 | alfalfa |
| <i>eurytheme</i> : | | | | | | | | | | | | | |
| Aug. 14-19 | 7.69 | ± 7.39 | 13 | 33.33 | ±12.17 | 15 | 21.43 | ±7.75 | 28 | 25.64 | 1.65 | >.05 | alfalfa |
| Aug. 21-22 | 8.70 | ± 5.88 | 23 | 0 | 0.00 | 9 | 6.25 | ±4.28 | 32 | 8.70 | .91 | >.05 | clover |
| <i>intermediates</i> : | | | | | | | | | | | | | |
| Aug. 14-19 | 23.08 | ±11.69 | 13 | 0 | 0.00 | 15 | 10.71 | ±5.84 | 28 | 23.08 | 1.97 | <.05 | clover |
| Aug. 21-22 | 8.70 | ± 5.88 | 23 | 0 | 0.00 | 9 | 6.25 | ±4.28 | 32 | 8.70 | .91 | >.05 | clover |

TABLE V. The frequency of *Colias philodice* (yellow), *Colias eurytheme* (orange), and intermediates in nearby alfalfa and red clover fields near Rockford, Illinois, Sept. 13, 1947. Percentage of total

| | Clover % | S.E. | N. | Alfalfa % | S.E. | N. | Location total % | S.E. | N. | Difference % | t | Probability | High freq. in field |
|---------------------------|----------|-------|-----|-----------|-------|-----|------------------|-------|-----|--------------|------|-------------|---------------------|
| ♂ | | | | | | | | | | | | | |
| <i>eurytheme</i> (orange) | 16.13 | ±6.61 | 31 | 86.54 | ±4.73 | 52 | 60.24 | ±5.37 | 83 | 70.41 | 6.34 | <.01 | alfalfa |
| <i>philodice</i> (yellow) | 77.42 | ±7.51 | 31 | 9.62 | ±4.09 | 52 | 34.94 | ±5.23 | 83 | 67.80 | 6.27 | <.01 | clover |
| intermediate | 6.45 | ±4.41 | 31 | 3.85 | ±2.67 | 52 | 4.82 | ±2.35 | 83 | 2.60 | 0.53 | >.05 | — |
| ♀ | | | | | | | | | | | | | |
| <i>eurytheme</i> (orange) | 38.46 | ±4.77 | 104 | 76.67 | ±3.86 | 120 | 58.93 | ±3.29 | 224 | 38.21 | 5.80 | <.01 | alfalfa |
| <i>philodice</i> (yellow) | 56.73 | ±4.86 | 104 | 15.00 | ±3.26 | 120 | 34.38 | ±3.17 | 224 | 41.73 | 6.56 | <.01 | clover |
| intermediate | 4.81 | ±2.10 | 104 | 8.33 | ±2.52 | 120 | 6.70 | ±1.67 | 224 | 3.52 | 1.05 | >.05 | — |

67.80 ± 10.82%. The difference shown in the frequency of the intermediates is not significant at less than the 5% level.

The female butterflies at Rockford, Illinois, do not show quite as great a difference in their proportions. The orange *eurytheme* was still more abundant in the alfalfa field but this difference was not as great as in the males, being only 38.21 ± 6.59% as against 70.41 ± 11.11% for the males. The yellow *philodice* was also more abundant in the clover field as shown by the difference 41.73 ± 6.36%. The difference shown by the intermediates was as in the males but was not significant at less than the 5% level.

A corresponding difference was apparent between the fields near Celina, Ohio (table VI). The orange *eurytheme* males were more abundant in the alfalfa field than in the red clover field as shown by the difference 19.54 ± 6.53%, and the yellow *philodice* males were more abundant in the clover field as shown by the difference 24.56 ± 5.59%. The difference observed between the fields in the

frequency of intermediates is not significant at less than the 5% level.

The females at Celina, Ohio, show a corresponding difference between the two kinds of fields which is significant in the case of *philodice* at the 5% level. The difference is smaller than the males, however, just as is the case at Rockford, Illinois. For *eurytheme* females the difference is 6.19 ± 5.27% as compared with 19.5 ± 6.53% and for *philodice* it is 9.91 ± 4.72% as compared with 24.56 ± 5.59% for the males. For the intermediates the difference is not significant.

DISCUSSION

The data presented above illustrate almost without exception that there is a predilection of *Colias philodice* for the red clover fields and *Colias eurytheme* for the alfalfa fields where these two species exist in the same general areas in southern Michigan, southern Ohio and northern Illinois. This is quantitative evidence of a view which has been held for some time as a general impression.

TABLE VI. The frequency of *Colias philodice* (yellow), *Colias eurytheme* (orange) and intermediates in nearby alfalfa and red clover fields near Celina, Ohio, Oct. 26, 1947. Percentage of total

| | Clover % | S.E. | N. | Alfalfa % | S.E. | N. | Location total % | S.E. | N. | Difference % | t | Probability | High freq. in field |
|---------------------------|----------|-------|-----|-----------|-------|-----|------------------|-------|-----|--------------|------|-------------|---------------------|
| ♂ | | | | | | | | | | | | | |
| <i>eurytheme</i> (orange) | 58.62 | ±6.47 | 58 | 78.16 | ±2.88 | 206 | 73.86 | ±2.70 | 264 | 19.54 | 2.99 | <.01 | alfalfa |
| <i>philodice</i> (yellow) | 36.21 | ±6.31 | 58 | 11.65 | ±2.24 | 206 | 17.05 | ±2.31 | 264 | 24.56 | 4.39 | <.01 | clover |
| intermediate | 5.17 | ±2.91 | 58 | 10.19 | ±2.11 | 206 | 9.09 | ±1.77 | 264 | 5.02 | 1.18 | >.05 | — |
| ♀ | | | | | | | | | | | | | |
| <i>eurytheme</i> (orange) | 73.81 | ±3.92 | 126 | 80.00 | ±3.51 | 130 | 76.95 | ±2.63 | 256 | 6.19 | 1.17 | >.05 | alfalfa |
| <i>philodice</i> (yellow) | 22.22 | ±3.70 | 126 | 12.31 | ±2.88 | 130 | 17.19 | ±2.36 | 256 | 9.91 | 2.10 | <.05 | clover |
| intermediate | 3.97 | ±1.74 | 126 | 7.69 | ±2.34 | 130 | 5.86 | ±1.47 | 256 | 3.72 | 1.27 | >.05 | — |

In addition to this general conclusion, these data show a few other facts which had not before been founded upon satisfactory evidence, and also show some points for which additional information is necessary before clarification is achieved.

The change in the frequency of orange *eurytheme* males from a high value in the alfalfa field to the clover field during and after the cutting of the alfalfa field and the reverse for the *philodice* requires explanation (table I). First must be considered the stimuli which draw the male butterflies to a field. Of these, the following seem to be important: (1) attraction by scent or sight to flowers in the field, (2) attraction by scent or sight to alfalfa as the larval food plant, (3) attraction to the field because of females of the same species in the field, (4) concentration in the field because of their emergence from the pupal case there, if an assumption be made that *eurytheme* must utilize alfalfa as larval food and *philodice* must utilize red clover as a larval food.

The first suggestion would be very difficult to analyze. Alfalfa flowers were present in the alfalfa field before cutting and clover blossoms were present all the time in the clover field. After cutting there were no more alfalfa blossoms available in the alfalfa field and therefore the butterflies would no longer be attracted there for that reason. If there were no attraction of the species for a specific type of flower, then the frequencies would not change before and after cutting. The yellow *philodice* could not be said to have been changed in attraction to the alfalfa field after cutting of the alfalfa because clover flowers were unchanged in availability throughout. Therefore, one may conclude that cutting would not in any case affect the absolute number of yellow in the clover field for this reason alone, but might affect the orange.

Less than one-third of the *Colias* butterflies in the Ann Arbor area are *eurytheme*, the greater proportion being the yellow *philodice*. If most of the *eury-*

theme are drawn from the alfalfa field by attraction to flowers in the clover field, the proportion of orange in the former field would seriously drop, there being no change in absolute numbers of yellow in either field.

The second explanation possible does not seem probable for cutting of the alfalfa field does not remove all vegetation and there is still a cover of green leaves present there.

The third explanation seems quite important for the impression has been gained that males are attracted to fields with many females, provided that they are those in which females are newly emerging. A male will copulate with many females but females rarely copulate more than once. This occurs generally very soon after emergence even while the wings are not yet dried enough for flying. Some fields have been seen with males swarming while some adjacent fields are nearly barren of them. The former are fields in which the pupae are hatching, and in these fields many copulating pairs may be found. If *eurytheme* females are more likely to be emerging in the alfalfa field than in the clover field, the males would be attracted there. Likewise, *philodice* males would be attracted to the clover field where *philodice* males would be hatching. If all the *eurytheme* pupae (attached to the alfalfa stubble) were removed from the alfalfa field at cutting, then the attraction to the field would cease and the *eurytheme* males would cease to be attracted there. Instead the *philodice* females might then be attractive to the *eurytheme* males in lieu of nothing at all.

The fourth explanation seems possible in very large fields but does not seem likely to be effective for any great length of time because the butterflies can be seen flying readily back and forth from field to field. They are thoroughly mixed up in a very short time.

A final answer can not be given to this phenomenon. In any event, the true answer probably combines all four of the suggestions made.

TABLE VII. *The difference between the different frequencies of orange eurytheme, males and females, in alfalfa and red clover fields. Percentage of total*

| | Michi- gan % | S.E. | N. | Ohio % | S.E. | N. | Illi- nois % | S.E. | N. | Aver- age Differ- ence % | N. |
|----------------------------------|--------------------|------------|-------------|-----------|-------------|-------------|--------------------|-------------|------------------------|--------------------------------------|-----------------------------|
| Males | 22.23 | ± 6.57 | 191 | 19.54 | ± 6.53 | 264 | 70.41 | ± 11.11 | 83 | 40.43 | 538 |
| Females | 25.64 | ± 15.55 | 28 | 6.19 | ± 5.27 | 256 | 38.21 | ± 6.59 | 224 | 20.71 | 508 |
| Difference of the differences | 3.41 | $t = .188$ | $p = > .05$ | 13.35 | $t = 1.596$ | $p = > .05$ | 32.20 | $t = 2.486$ | $p = < .05$ $> .01$ | 19.72 | 1046 = 3.203 $p = < .01$ |

A second point which can be noted in the data is the much greater differential segregation of the males than the females in the alfalfa and red clover fields. These data are shown in table VII. The difference is not observed in Michigan (probably due to the small numbers), is present in Ohio and is especially marked in Illinois. The totals of the males and the females and the differences between them are 40.43% males and 20.71% females with a difference of 19.72% which is significant at about the 0.3% level.¹ Therefore, there seems to be reason to inquire if the males do not show a greater specificity for habitat than do the females.

It has long been the impression of the author that the females of *Colias* wander farther away from the place of emergence than do the males. This impression may have been formulated by observing more males always in fields where the adults are emerging, the females leaving the fields soon after emergence and copulation. Likewise, concentrations of worn and apparently sexually unattractive females have been observed in fields remote from emerging fields. If these facts

¹ The test of significance of the difference between these differences has been calculated from the following formula

$$t = \frac{(\bar{p}_1 - \bar{p}_2) - (\bar{p}_1^1 - \bar{p}_2^1)}{\sqrt{PQ \left(\frac{1}{N_1} + \frac{1}{N_2} + \frac{1}{N_1^1} + \frac{1}{N_2^1} \right)}}$$

where

$$P = \frac{N_1 \bar{p}_1 + N_2 \bar{p}_2 + N_1^1 \bar{p}_1^1 + N_2^1 \bar{p}_2^1}{N_1 + N_2 + N_1^1 + N_2^1}$$

and \bar{p} equals the male frequency, \bar{p}^1 the female frequency, \bar{p}_1 the frequency in the alfalfa field and \bar{p}_2 the frequency in the red clover field.

are accounted for by the wider ranging abilities of the females, then the data as presented in table 7 may also be accounted for in the same way. The males may tend to remain in the field of their emergence because of the attraction to the emerging females. The females do not have an equivalent attraction and disperse over the countryside. They should be attracted to their larval food plant for egg laying but this attraction does not seem to be strongly differential over a wide area. Females have been seen to lay their eggs on many kinds of leguminous plants other than those normally used as food. The question may be summed up in the following statement: the males are more strongly attracted to the fields of their larval food plant than are the females; this attraction may be toward the emerging females in that field rather than for the food plant itself; the females may wander more than the males and be attracted to fields of clover or alfalfa in the search for plants upon which to lay their eggs; thus the females may be found in both types of fields while males are concentrated more in only one type. This does not negate the attraction of the females for the food plant of their larval choice for the attraction may be in a wide sense for fields of legumes as contrasted with fields of grains or of vegetables.

SIGNIFICANCE

Colias eurytheme and *Colias philodice* are interfertile butterflies² which occupy

² *Colias eurytheme* and *Colias philodice* have been tentatively classified as distinctive types of *Colias chrysotheme* by numerous authors includ-

a wide geographical range throughout North America. The distribution of each includes areas which are not occupied by the other. Half the area occupied by *philodice*, however, is also occupied by *eurytheme* and about three-fourths of the area occupied by *eurytheme* is also occupied by *philodice*. Hybrids are formed as the result of intercrossing of the two (Gerould, '43) and these hybrids are inter-fertile with the parental types and intra-fertile with other hybrids. As a result of the wide range of crossing and the multiple factor genetic difference between the species, a complete range of intergrading forms may be found in any location where the two species exist together (Hovanitz, '43b). Hybridization of the two species has been known to have occurred at least sixty years ago under natural conditions and is at present of such frequent occurrence that the genetic consequences should be the complete obliteration of both species in favor of an intermediate form. The data do not indicate any such result however. The maintenance of each species as a separate entity continues.

Two factors may be instrumental in maintaining this continued hybridization of the two species and the preservation of the genomes typical of each. The first is a sufficiently lowered viability of the hybrid products so that they are at a disadvantage over the parental types. Data have been obtained on some lowered viability of this type but nonetheless most

intermediate products are perfectly viable and fertile on a par with the parental types (Hovanitz, '44). Lowered viability, if due to the recombination of nonharmonious gene systems, would not persist long if harmonious systems were developed which were intermediate between the parental types. A new intermediate species might be formed by elimination of the parental types.

The second factor which may be instrumental in maintaining the two species relatively distinct is ecological segregation. If the populations of the two species inhabiting the same general area were largely separated by confinement to different habitats, the sexes of the two species would find it difficult to find a mate of the other species. A mechanism of this sort is also apt to be broken down readily enough by hybridization, however. Habitat preference by organisms is a complex physiological adjustment, requiring the selection of genes most suitable for the survival of the organism. These genes would be reassorted by hybridization and the gene combinations upon which ecological isolation depends would cease to be maintained. Something necessary to the survival of each species is required in order to prevent intercrossing from amalgamating the two into one. This factor is probably the larval food plant specificity (Hovanitz, '44).

Colias philodice does not find alfalfa (*Medicago sativa*) a suitable larval food³ and *Colias eurytheme* does not find red clover (*Trifolium pratense*) a suitable food. Both can utilize white clover (*Trifolium repens*) however. Throughout much of the present range of the two species, red clover is the larval food plant of *C. philodice* and alfalfa is the larval food plant of *C. eurytheme*, while white clover

ing Hovanitz, 1943a. As was then stated, "The use of the binomial or the trinomial name in this group must remain a matter of convenience depending upon the use to which the name is put." Since further information on other species of *Colias* indicates that hybridization and interfertility is of general occurrence in this genus even under natural undisturbed conditions, the names *philodice* and *eurytheme* may be used as binomials without implying that they are completely separated reproductively. As was noted in 1943, the name *philodice* may be used for all the yellow forms of the *chrysotheme* complex with the subspecies *philodice*, *hagenii*, *eriphyle*, *vitabunda* and *guatemalena* forming geographical counterparts.

³ Since this paper was written, a yellow race of *philodice* with orange on the hind wings frequently has been observed on alfalfa in southeastern Colorado (Arkansas valley). Here it is as abundant (August 1948) on alfalfa as is *eurytheme* on the same plant in California. Fields swarm with adults and larvae.

is used sparingly by both. Sterility or abnormal development may be the result of exchanging these normal plants (Hovanitz, '44). Hybrids can develop normally on either (Gerould, '43; Hovanitz, '44) but to what extent all hybrids do so is not yet known. Here at least is an isolating factor that is sufficient to separate the two species into distinct habitats where these plants are grown.

The data given in this paper provide one further step to understanding the nature of the mechanism which is maintaining these two species as relatively disjunct entities.

ACKNOWLEDGMENT

The writer is indebted to C. C. Craig of the Statistical Research Laboratory of the University of Michigan for suggesting the tests of significance used in this paper. The calculations were performed by the service.

SUMMARY

1. The relative proportions of the yellow butterfly *Colias philodice* and the orange butterfly *Colias eurytheme* and in-

termediates between them were determined in adjacent or nearby alfalfa and red clover fields in southern Michigan, southern Ohio and northern Illinois.

2. There is a higher proportion of *eurytheme* in alfalfa fields and *philodice* in red clover fields in each of these places.

3. The males seem to be more selective than the females for the two kinds of field.

4. Cutting of one of the alfalfa fields changed the relative proportions of the species found in the fields.

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TERRON VEGETATION IN NEW MEXICO¹

ALTON A. LINDSEY

Biology Department, Purdue University

INTRODUCTION

Terrones are earth construction bricks cut directly from the natural sod of sedge meadows, and dried in the sun. Such bricks have been used for several hundred years in the Rio Grande valley, and today are produced commercially by Spanish and by Indian workmen. They are used chiefly by these two population groups, but to some slight extent by "Anglos" also. Although terrones are familiar objects to thousands of New Mexicans, we have been unable to find any reference to them in scientific, architectural, or popular writings, except that Weaver and Clements ('38, fig. 50) published a photograph of a terron field with the legend "Subseria alternans in New Mexico due to the removal of sod for adobe houses, . . ." It will be pointed out later why use of the term "adobe" in this connection is contrary to southwestern usage.

The cohesiveness of terrones is determined by the nature and abundance of the plant roots and rhizomes which bind the earth, and the texture of the soil itself. A heavy clay with abundant fine grass roots makes the best terrones, but even a sand containing as little as 15 per cent of clay and silt combined can be consolidated sufficiently by twenty years of plant growth. Experienced terron-cutters state that the abundance of roots is more important than the texture of the soil. Fibrous roots of grasses are most effective in binding the mineral particles. The most frequent terron plant is salt-grass, *Distichlis stricta* (Torr.) Rydb.

¹ The investigation was made during the summer of 1947. The writer thanks Messrs. Ben Garcia, Manuel Tafoya, Joe Lopez, Wm. Wagner, Richard Pugh; J. A. Williams of the Soil Conservation Service, and the staff of the U. S. National Herbarium. Dr. D. B. Lawrence kindly made the final draft of figure 1.

It spreads rapidly by tough rhizomes in the upper two inches of soil, sending down a dense growth of fine roots farther than the depth to which terrones are cut, which is either six or four inches, for spade-cut, and machine-cut bricks, respectively.

The terron fields studied are situated in alluvium along the middle Rio Grande north and south of Albuquerque, N. Mex. (fig. 1). Because at present most terrones are being produced near Isleta and Los Lunas, 13 and 21 miles south of Albuquerque, particular attention was

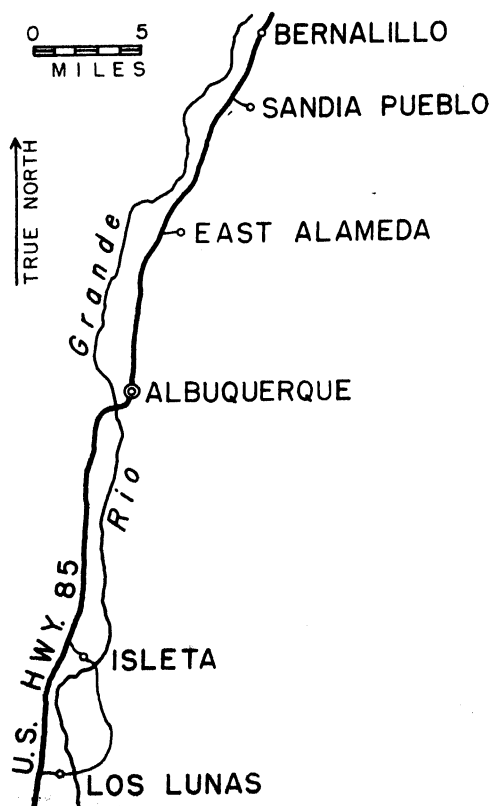


FIG. 1. Map showing locations of the towns in the Rio Grande valley, New Mexico, in the area where terrones are most used.



FIG. 2. Terron removal from previously uncut surface. Stacks of drying bricks appear in the right background.

given terron fields in this stretch of valley. At Isleta extensive ones are in production both east and west (fig. 2) of the river. All fields studied had been protected continuously against grazing.

The National Resources Committee ('38) has published meteorological data obtained by the Bureau of Agricultural Engineering at an evaporation station at Isleta during June to November, inclusive, of 1936. The rainy season in this region comes within this period of the year. The location makes the data highly applicable to terron vegetation, since the station lay within a mile of both the Isleta terron fields, and nearly equidistant between them. Within a radius of sixty feet from the evaporation pan, vegetation tanks for saltgrass, sedges, and cattails were placed. For the six month period, precipitation totaled 6.04 inches, while evaporation from a free water surface amounted to 44 inches. Wind movement averaged 2.52 miles per hour, and the mean temperature (at Albuquerque 13 miles distant) was 66. Under these conditions, consumptive use of water by the saltgrass in a tank two feet in diameter,

with an average depth to water of 7.7 inches, was 23.5 inches. From another tank containing *Carex* sp. and *Eleocharis* sp., in which the water level was maintained at the soil surface, 50 inches were lost in the six months of record. Consumptive use by cattails under the same conditions was 67.7 inches, or 154 per cent of the water depth lost from the open evaporation pan. On the basis of the 1936 data, the precipitation/evaporation ratio in the Isleta terron fields for the summer and fall months was only 0.14. Since the recorded precipitation for this period is about three-fourths of the usual annual precipitation, it is evident that the P/E ratio for the year runs even lower.

SUCCESSION

The natural plant community ready to yield high quality terrones represents a late, relatively dry sedge-meadow stage of the hydrosere, usually dominated by saltgrass and containing much *Juncus balticus* var. *montanus* Engelm. Figure 3 shows one of the square meter quadrats in an Isleta field, uncut for at least thirty years.

Let us trace the course of succession in a field from which the upper six inches of soil has been removed, to the mature saltgrass meadow ready to supply another crop of good terrones. The recently bared earth in the fields south of Albuquerque shows an efflorescence of dried "white-alkali" containing gypsum and other salts. The depth of the water table, averaging fourteen inches in July and twenty-one in August, is determined by the river rather than by local rainfall. In all the terron fields observed, only one plant invades in numbers the first year after cutting. This is the annual composite *Flaveria campestris* J. R. Johnst. The plant averaged 74 individuals per square meter by mid-July, in a field cut six months previously. No other species had yet appeared.

Late in the first growing season after terron removal, a very few small scattered saltgrass plants make their appearance. Seeds are not important in their return and no propagation from old root systems was noticed. The new growth sprouts

from the few abnormally deep rhizomes which remained below the skinned surface. In the second and third years "sedge-grass" (*Triglochin maritimus* L.) is abundant, but became infrequent or absent later, due to competition with the well established saltgrass.

It was possible to date precisely only four areas which the terron cutters had worked more than three years before. On one of these, we had watched a full-time terron-cutter of Isleta working four years previously. A field four years older was identified by him as having been cut in 1939. Another field was dated by two workmen independently as one which they had helped cut over during the summer when the adjacent highway was paved, which was 1933. A typical square meter there is shown in figure 4. The oldest area studied had never been cut within the memory of any of the workmen; it had certainly not been worked for at least 30 years. Possibly it had been used before that by Indian cutters from the Isleta Pueblo; if so, it had completely

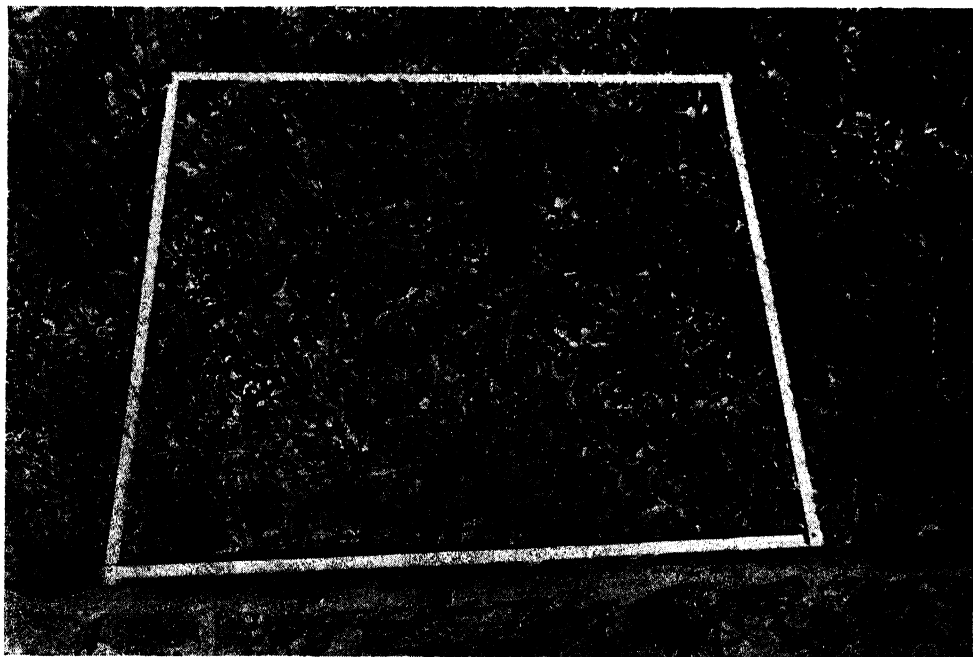
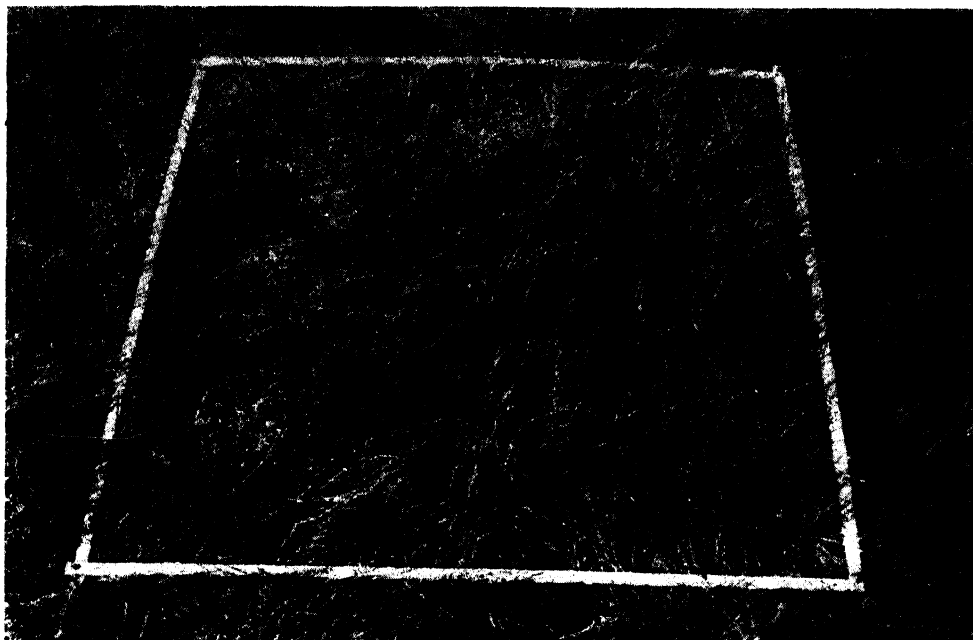


FIG. 3. Square meter in uncut area; *Distichlis* and *Anemopsis* are conspicuous.

FIG. 4. Square meter in fourteen year *Distichlis* cover.

recovered and may be considered, for our purpose, an uncut area.

Table I shows the average numbers per square meter of the principal species on each of these four areas as determined from square meter count-list quadrats in the rather uniform vegetation. Due to the scattering of the slender aerial parts of the grass, sedges, and rushes, the basal area method was not applicable. Clip quadrats might have been used to indicate relative importance of species by dry weight. However, since grazing use is not an object here the forage yield is of little significance. The interest focuses on the sub-surface parts of terron plants; the number of scattered aerial parts correlated better than their dry weight with the extent and binding power of the root systems. For example, *Eleocharis* and *Anemopsis californica* (Nutt.) Hook. and Arm. occur together in the mature sedge-meadow stage, and the total dry weight of the former's aerial parts is negligible compared with the massive *Anemopsis*. Yet the rhizomes and numerous fine rootlets of *Eleocharis* and *Juncus* make

these genera much superior to coarse herbs in terrones.

Since terron species have vigorous rhizomes or stolons, and offspring connected to the parent, the entire "plant" is not a suitable unit for quadrat counts. Separate aerial stems were counted, except for *Distichlis* and *Anemopsis* in which the tuft is the most feasible unit for above-ground counts. In saltgrass a tuft is the closely bunched group of culms, or occasionally only one culm, derived from one point on the rhizome. In *Anemopsis* the large basal leaves develop long before the flowering stem; the unit

TABLE I. Average numbers per square meter in four areas of different ages since terron removal; based on 14 quadrats

| | 4 years | 8 years | 14 years | Uncut area |
|---|------------|------------|-------------|---------------|
| <i>Distichlis stricta</i> (tufts) | 538 | 322 | 902 | 926 |
| <i>Juncus balticus</i> | 95 | 163 | 0 | 347 |
| <i>Scirpus americanus</i> | 31 | 499 | 52 | 0 |
| <i>Anemopsis californica</i> (tufts) | 0 | 0 | 0 | 81 |
| <i>Eleocharis</i> sp. | 0 | 19 | 0 | 352 |

here is the parent plant, or a leafy, usually rooted, rosette along a stolon, or a detached offspring. Since two different units were required for the various life-forms represented in table I, the valid comparisons are those between different age classes of the same species, and between species counted on the same unit basis.

This table shows that *Distichlis* is by far the most important terron species. It may be assumed that if a given quadrat had been followed through for fifteen years there would have been a continuous increase of saltgrass tufts. The absence of a marked difference in its numbers between the 14 year and uncut areas may be explained by the increase of *Juncus* and *Eleocharis* and the advent of the aggressive broad-leaved *Anemopsis*. The saltgrass is much shorter in height in the uncut area than in the other three areas tabulated. *Scirpus americanus* Pers. is the only important terron plant which is not more abundant in the uncut area than in the younger areas.

The stages of typical succession may be summarized as follows: (1) *Flaveria*, (2) *Triglochin-Distichlis*, (3) *Distichlis-Scirpus*, and (4) *Distichlis-Juncus-Anemopsis*.

Among the minor plants in terron fields, flowering *Aster pauciflorus* Nutt. was prominent in the July aspect of the 8 year area only. *Triglochin* is found rarely in the 4, 8, and 14 year areas, but is absent in the uncut area. Young plants of the pioneer *Flaveria* occur rarely in the uncut area, but never reach the flowering stage there. A few shrubs and young trees were scattered widely in the 8 and 14 year fields; some in the latter had reached six years of age. The species are *Populus wislizeni* (Wats.) Sarg., *Elaeagnus angustifolia* L., and *Baccharis salicina* Torr. and Gray. In terron fields at Isleta Marsh, an area cut about three years before was covered throughout with a dense stand of young salt-cedar (*Tamarix gallica* L.), while none occurred in adjacent areas cut at various other times.

Of the four woody species, the salt-cedar is best able to withstand "white-alkali" and submergence of its roots for long periods. A good terron field is too wet a habitat for the other woody species to thrive.

Communities occupy low "white-alkali" swales along the Rio Grande where the water table, fluctuating with the height of the river, averages much higher than in most terron fields, and often stands over the soil surface. The dominants *Scirpus americanus* and *Aristida* sp. grow three feet tall, or six times the plant stature in typical terron fields. Scattered *Typha latifolia* L. remain in these wet sedge-meadows as relicts of the reed-marsh stage. Terrones in such spots are always cut by spade rather than machine.

On clay alluvium near the Sandia Pueblo 15 miles north of Albuquerque, irrigation is practiced for the encouragement of the natural growth for terron production. The dwellings, barns, and walls in Sandia village are built of terrones; it is likely that bricks have been cut from this field for hundreds of years. Under occasional heavy surface flooding from an adjacent irrigation ditch, a very different type of vegetation occurs than on the sandy, salty, high water-table fields of the Isleta region. The main species in the brown heavy Sandia terrones, in decreasing order of abundance, are: *Poa fendleriana* (Steud.) Vasey, *Juncus balticus* var. *montanus* Engelm., *Carex douglasii* Boott. and *Potentilla anserina* L. After cutting, *Flaveria campestris* and *Potentilla* make very slow growth during the first and second years. The oldest recognizable cut-over area is at least six years; no appreciable revegetation by grasses has taken place. The whole cut-over field is very bare. While irrigation benefits the terron vegetation in the uncut places, the natural water table, which has dropped in recent decades due to drainage ditches, is too low for re-establishment of terron species even with some irrigation.

PLANT CONTENT, PROPERTIES, AND USE OF TERRONES

Samples of soil of commercial terrones from Isleta and Sandia Pueblo were submitted to the Soil Conservation Service laboratory in Albuquerque. The analyses are summarized in table II, which shows averages of the values obtained. Percentages given for total soluble salts are means of the results of two methods, bridge salt determinations made on a soil paste having a moisture content approaching the water holding capacity of the soil, and gravimetric on a 1-20 soil-water ratio. One of the Isleta terrones had a salt content of 1.83 per cent.

TABLE II. *Properties of terron soils. Figures are per cent, except pH values*

| | Sand | Silt | Clay under .002 mm. | Clay under .005 mm. | Total sol. salts | pH |
|-------------|------|------|------------------------------|------------------------------|------------------------|------|
| Isleta soil | 67.5 | 16.5 | 16 | 20.5 | 0.90 | 7.67 |
| Sandia soil | 10 | 51 | 39 | 68 | 0.36 | 7.15 |

An entire Sandia terron measuring 14" × 10" × 4", consolidated by *Poa* and *Anemopsis*, was soaked for a week, then kneaded thoroughly while a sharp stream from a garden hose played on it, until all soil was removed and the water ran clear. Although the thickness now bulked a fourth of the original thickness, the intact root mass maintained the original rectangular outline despite the rough treatment required to eliminate the heavy clay soil. The dried roots and rhizomes weighed 3.82 per cent of the dry weight of the soil alone. The age of the vegetation of the Sandia terrones is unknown.

By the above method of separating soil from plant parts, many of the finest rootlets were lost. In order to compare the underground plant development in some of the above-cited quadrats of various known ages, the following method was used to prevent the loss of fine rootlets. The entire fresh-cut terron was weighed, then sliced into pieces about one inch thick. The slices were broken and

kneaded under water in a large tub to clean and remove all the rhizomes and roots. The sediment was strained repeatedly with coarse and fine sieves to recover the fine rootlets, and all the water carefully strained. The material was then rinsed in clean water and again separated by sieves. About a day was necessary for working out one terron in this way. After storage until the plant parts were dead and air-dry, they were further dried by the intense sun in calm dry air. The dry weight of the terron soil was calculated from data on a large soil sample taken at the same time from just adjacent to the terron, later sun-dried in a thin layer.

Two terrones from a quadrat in the 4 year area were thus analyzed. This square meter had contained 543 tufts of saltgrass and 122 stems of *Scirpus*. The total weight of the roots and rhizomes comprised 0.44 per cent of the weight of the soil alone.

The square meter shown in figure 4, in the 14 year terron field, supports 902 tufts of saltgrass. In a terron dug from this same quadrat, the underground plant parts totalled 0.82 per cent of the weight of the soil itself.

The soil in the 14 year area is exceptionally sandy; placed in water the sand fell away from this terron so that the root systems were shaken out easily. Although the number of rhizomes was about double that in the four year area, the fine rootlets were much less abundant. This proved general for the 14 year area; terrones from it were much less cohesive than those from the 4 year area which contained more silt and clay. The root difference would not be suspected from examining the plant tops, since the grass in figure 4 appears much better developed than that in the 4 year area (cf. table I). Terron cutters consider six years as the average time required for a cut-over area to grow a new crop of terrones. Part of the 14 year area was cut again in 1946 after thirteen years, but the terrones proved worthless and were left stacked in



FIG. 5. Face of vertical cut through a terron six inches thick, showing rhizomes *in situ*.

the field. Old Spanish residents told the writer of a practice before the turn of the century, when terron was the principal building material used in this stretch of the valley, except in Albuquerque, and many men made a living by terron-cutting.

When the river was in flood they would turn the flood waters into the terron fields in order to build up deposits of silt and clay around the plants and thus increase the compressive strength of future terrones.



FIG. 6. Pile of roots and rhizomes only, removed from a terron equal in size to that shown, i.e., 14" \times 6" \times 6".

A terron was taken from the quadrat, typical of the uncut area, which is shown in figure 3. A smooth cut was made lengthwise in a vertical plane, and about a quarter-inch of the soil washed off the cut surface with a hose, to show the distribution of the rhizomes in a bisect (fig. 5). This same brick yielded the pile of subsurface plant parts shown in figure 6, which weighed 3.35 per cent of the soil weight. The terron that yielded the plant material was equal in size to the one shown there for comparison.

Several terrones which had been air-dried for three years were sent to a materials testing laboratory where they were prepared for and subjected to a machine compression test by the standard method for testing adobe brick for building-code specifications. Three saltgrass terrones from Isleta showed a strength in compression of 189, 172, and 164 lb. per square inch, averaging 175 lb. A *Poa* terrone from the Sandia field tested 252 lb. per square inch. The adobe (molded) bricks regularly tested by this laboratory average approximately 250 lb.

Many Spanish-Americans in the middle Rio Grande valley strongly prefer terrones over adobes because of their reputation for withstanding flood waters, which rapidly dissolve adobe houses. We submerged a thoroughly hardened, good quality adobe brick, weighing 29.5 lb., in water. Its surface began disintegrating at once. By the end of 2.5 hours the adobe had fallen apart completely, leaving no solid fragment. In contrast, one Isleta and one Sandia terron were kept submerged for thirty days; following which there was no indication that any soil whatever had been lost, the edges and corners remaining as sharp as before. Another saltgrass terron thoroughly saturated after soaking for twelve days, bore a weight of 620 lbs. with very slight visible compression that resulted only in squeezing a little water from the brick. This weight is twice that of the wall upon a brick of the bottom tier. Usually, because of the much better bond obtained, clay mud is used in place of cement mortar in laying up the bricks; in this case the vulnerable point during a prolonged flood



FIG. 7. Unplastered terron house of type common in rural valley land near Albuquerque.

would be the mud mortar rather than the terrones.

The Spanish word "terron" has a more general meaning also—a clod, or small mass of soil. Terron bricks are not called "adobes" by the Spanish or Indian peoples, nor by other southwesterners who know how the two are produced. Adobe bricks are made by molding a wet earth mix in wood frames. They contain very little organic matter except the added straw which is traditionally believed to strengthen the brick, but, according to Eyre ('35), reduces the compressive strength 52 per cent. Examination of a terron wall reveals the dead rhizomes and roots, *in situ*, in the inverted terrones. Most terron houses have the bricks exposed to the elements; figure 7 shows a typical small but well-constructed house. A number of large, modern, well-built homes constructed of terrones covered with stucco were located. Terrones cost \$25.00 per thousand, or one-third the cost of adobes. The present Spanish village of East Alameda, just north of Albuquerque, was built of terrones in 1874. The old mission church at Isleta, which was built before

1629, and is in use and good condition to-day, is stated by the Indians to be (as is the rest of the village), of terron construction, but the plaster prevents confirming this.

SUMMARY

Natural sod of sedge-meadows along the middle Rio Grande is cut into terrones, sun-dried and used to construct buildings and walls. Saltgrass (*Distichlis stricta*) and *Juncus balticus* largely contribute the roots and rhizomes binding terron soils. A typical cut-over area undergoes a succession of four stages. The dry weight of the subterranean plant parts in terrones ranges up to 3.8 per cent of that of the soil alone. Four terrones tested for compressive strength averaged 194 lb. per square inch.

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OBSERVATIONS ON A POPULATION OF THE SALAMANDER, *AMPHIUMA TRIDACTYLUM* CUVIER *

FRED R. CAGLE

Department of Zoology, Tulane University

The life history of the salamander, *Amphiuma tridactylum* Cuvier, is poorly known and only scant information is available on population density or movements. Baker ('45) has summarized the literature and added much to our knowledge of this species. *Amphiuma* is abundant in the vicinity of New Orleans and the nearby towns where a blend of a high water table, loose surface soil and shallow drainage ditches furnishes an excellent habitat for this burrow-inhabiting, aquatic animal. The large populations supported in some ditches constitute the dominant vertebrate life. •

The salamanders are exceptionally abundant in Audubon Park across the street from the Tulane University campus. The park is bounded by a compact residential area on three sides and by the levee of the Mississippi River on the other (figure 1). A golf course in the northern half of the park is surrounded on two sides by a lagoon and is crossed by many shallow (2-12 inches deep) grass-lined drainage ditches. The entire area is closely mowed and well drained.

The water table in the park remains near the soil surface the year round. During heavy rains much of the golf course is flooded with several inches of water that remains for 1-6 hours after the rain ceases falling. During this period of brief flooding the *Amphiuma* are active in the shallow pools where they find a ready supply of food. The dark animals, conspicuous in the clear water against the smooth carpet of grass, may be easily collected.

I am indebted to the following students for aid in the collecting of the field samples discussed here: Mr. A. H. Chaney, Mr. W. Bright, Mr. A. Hale and Mrs.

Jane Spauschus. I am especially grateful to Mr. Cyrus Crites for his preparation of figures 5, 6 and 7.

PROCEDURE

The park was surveyed for the presence of *Amphiuma* on 32 trips, 24 night trips and 8 day trips in the period February, 1946 to December, 1947. Of the more than 500 animals observed, 112 were marked and released and 390 examined and preserved for future study.

The released individuals were sexed, measured, weighed and marked. The weighing and measuring of these long, muscular, slimy-skinned animals is difficult. Although repeated attempts to improve the accuracy of measurements of live animals were made, the body length and tail length could be measured only to the nearest centimeter. Anesthetization was not attempted as its effect on the animals after release was not known. The animals were weighed by placing them in a cloth sack on the scales. Animals retained in the laboratory were dissected to obtain information on stomachs and gonads.

It was desired to mark each animal so as to insure its recognition on recovery. A hand tattoo device was ineffective because of the rapid secretion of slime from the skin glands. Numbered celluloid tags supported by a nickel pin thrust through the tail muscles were used to identify 63 animals. These tags, used by the U. S. Fish and Wildlife Service to tag shrimp, could be placed in position easily and rapidly with little injury to the animal. Tagged *Amphiuma* retained in the laboratory had no harmful effects from the nickel pin penetrating the tail muscles, but the only one recovered from the field had mud and debris packed around the metal pin and celluloid tag and the tail much lacerated. The slight projection

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FIG. 1. An aerial view of Audubon Park. The area studied is bounded by a white line. The white rectangles are areas bounded on the basis of the drainage pattern for the purpose of placing the collection site of marked and released individuals. A pattern of shallow drainage ditches criss-crossing the southwest end of the golf course is evident.

formed by the tags was sufficient to entangle vegetation and debris through which the animal burrowed.

The tags were abandoned as unsuccessful and individuals were marked by a combination of tail notching to indicate groups and leg clipping to indicate specific individuals. Black tattoo ink was added to the tail notches to insure recognition on recovery. Of 49 so marked, 8 were recovered but none could be identified except by the tail notch, a group mark (figure 6). Salamanders marked by removal of toes and limbs could not be distinguished from individuals mutilated in fighting.

The marked animals were released at two points in the park, point 3, section E and point 4, section D (figure 1). Specific collection areas were recorded for only 31 of the animals released but all were collected from the golf course.

COLLECTING METHODS

The planned research required that the salamanders be captured in large numbers. Several types of traps were used experimentally. Mr. Alfred Hale, a graduate student, used net traps, hardware-cloth traps, snap-traps and trot lines with little success. The net traps were made of $\frac{1}{2}$ inch mesh netting supported on wire hoops 8 inches in diameter. A funnel throat was provided at each end. Only one salamander was captured in these traps.

A box trap constructed from hardware-cloth produced no better results. The wire was formed into a rectangle two feet long and eight inches square and a wire funnel inserted in one end. Bait was suspended above the funnel end. These traps yielded only 6 individuals in 936 trap hours. Fish and various kinds of

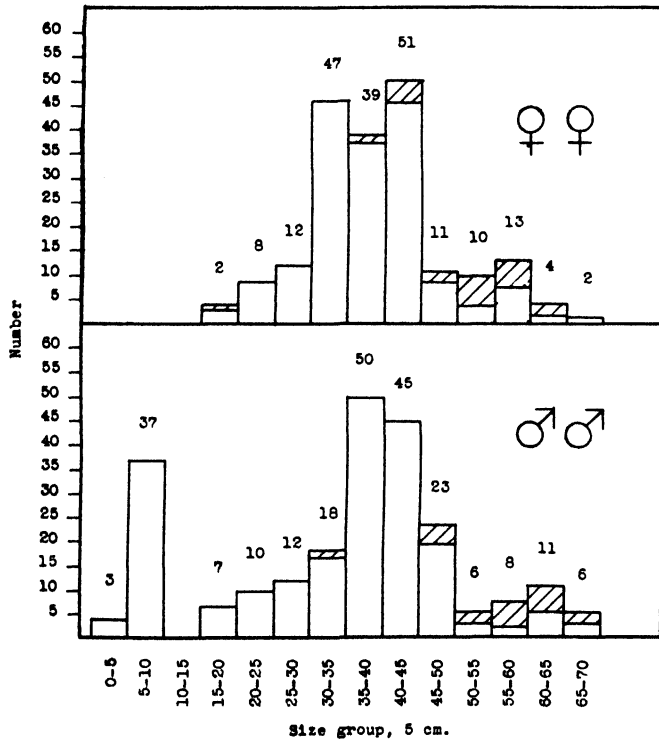


FIG. 2. The distribution of body lengths of 350 individuals (177 males; 173 females) from Audubon Park (unshaded sections) and 45 (shaded sections) from other areas.

meat were used as bait but *Amphiuma* chopped into inch-long sections produced the best results.

Baited hooks on individual lines were used with no captures (16,300 hook hours). The lines were often found with the bait removed and the lines twisted and torn. Baited lines were successfully used in a drainage ditch at Waggaman Pond near New Orleans. These lines were connected to a leader so that the twisting motions of the feeding salamander could not win their release. *Amphiuma* were often caught on trot lines set for turtles.

Hand collecting was the most profitable procedure. One man could flip the animals onto the bank where they could be captured or they could be picked directly from the water if the collector wore a rough-surfaced glove or wrapped a bit of burlap about his hand. This latter method proved to be very satisfactory.

THE POPULATION

The apparent unusual abundance of these animals in the Audubon Golf Course may well be a mere reflection of the ease of collecting. In the other habitats from which collections were made the observation and collecting of individuals was much more difficult. There is thus but scant basis for considering the park population

as exceptionally large. The drainage ditches and swamplands of the surrounding region may harbor as great a concentration per unit area.

A frequency distribution of body lengths (figure 2) of all the individuals measured in the laboratory indicated that 130 (75.1%) of the females were in the size range 30–45 cm. Within the three size groups of this range the females were nearly evenly distributed. Similarly the bulk of the males, 95 or 53.7%, occurred in the size range 35–45 cm. The four size groups in the range 30–50 cm. include 74% of the males collected.

This concentration of individuals in these size groups was tentatively interpreted as reflecting seasonal collecting but a plotting of length distributions for each month indicated that a similar concentration in these size groups occurred in each monthly sample when more than 20 were captured (figure 3). The abundance in this size range may be a result of the collecting procedures. Most of the collections in Audubon Park were made from the shallow ditches and pools. The lagoon and mouths of the ditches were not explored routinely as collecting was difficult in the deep water. The large adults (40–70 cm. in length) were usually collected from such places. The greater relative

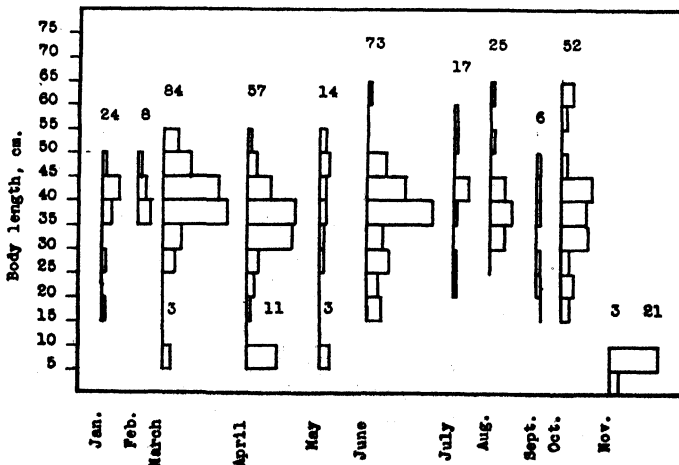


FIG. 3. The frequency distribution of body lengths of individuals (sexes combined) collected in each month.

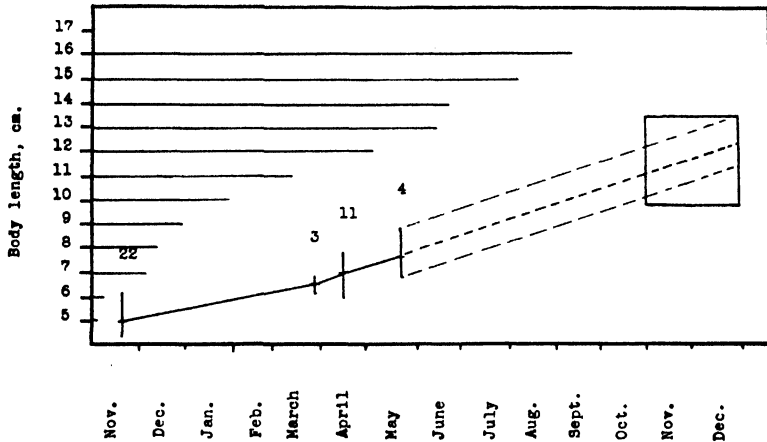


FIG. 4. The growth of young *Amphiuma* during the first season. The size range of juveniles in November and December is indicated by the area inclosed in the square.

abundance of large individuals in other areas (figure 2) suggests that the collecting procedure in Audubon Park may be the explanation but stresses also the possibility of a real difference in size distributions between the park population and that of other areas.

Collecting difficulty certainly is reflected in the frequency of occurrence of the smaller individuals. These are much more difficult to see as, unlike the larger ones, they readily find shelter in the grass and thin layers of debris on the bottom of the pools and ditches.

The former abundance of large individuals in the park has been stressed by Dr. F. H. Wilson who collected *Amphiuma* from the lagoons over a period of many years. Prior to 1942 he regularly collected individuals with a body length of 60–70 cm. Such animals are now rare in the park. Dr. Wilson has suggested in conversation that this disappearance may have resulted from the elimination of the thick aquatic vegetation, mainly alligator grass and water hyacinth, from the lagoon by the park authorities.

None of the more than 500 individuals collected had a body length greater than 70 cm. *Amphiuma* have been reported substantially larger than this. Baker ('45) states that they may reach a total

length of 40 inches (101.6 cm.) which represents a maximum body length of 73.6 to 84.6 cm. Baker ('47) presents a size distribution in which about 29% of the individuals had a body length in excess of 70 cm., the largest measured from Audubon Park. *Amphiuma* may attain an exceptionally large size in other areas in Louisiana. One individual so large in diameter that it was necessary to grasp it with both hands was lost in a swamp pool north of New Orleans after three men had attempted to hold it. This animal was much larger than any previously observed.

Of the 350 individuals greater than 15 cm. in body length (figure 2) 173 were females and 177 were males. This is not a significant deviation from the anticipated 50:50 ratio. All large samples contained approximately equal numbers of each sex. The absence of individuals in the size group 10–15 cm. obviously represents a failure to collect these individuals. As November and December were the only months when large samples were not taken, it was assumed that the growth pattern was such that young of the year reached the size range 10–15 cm. during these months. An extrapolation of the growth curve for hatchlings (figure 4) on the assumption that growth may be uniform during the first year indi-

cates that young of the year should be in the size range 10–14 cm. in November and December.

ACTIVITY

The animals are primarily nocturnal. When sufficient water is present (1–3 inches) in the ditches for them to move about, they emerge from the burrows in three or four hours after sunset and move slowly along the bottom seeking food. When sufficient food has been taken, they retreat to the burrows. Occasional individuals may be seen moving about on dark days or in early morning after a heavy cold rain.

The peak of the daily activity is usually reached between 10 and 12 P.M. Counts were made of animals observed during each hour of the night on several collecting trips in 1945 and 1946. Of the 236 individuals observed outside burrows 22 were seen between 9 and 10 P.M.; 115, 10–11 P.M.; 66, 11–12 P.M.; 16, 12–1 A.M.; 17, 1–2 A.M. In the early evening and early morning they rest quietly in the burrows with the tip of the head or about one quarter of the body projecting. From such positions they will strike at passing crawfish or fish. The skillful collector can sometimes capture such animals by driving a hook through the jaw or by grasping them tightly enough to pull them from the burrow. Ordinarily, however, the animals are alert when in such position and slide rapidly back into the burrows at the slightest disturbance.

Activity occurs after rains throughout the year. Large collections were taken during every month when collecting was attempted. As the water temperatures drop the salamanders become more sluggish but continue to leave the burrows and feed until temperatures are lower than 9° C. Collections were made several times from water at a temperature of 9–12° C. but when water temperature reached 5° C. no animals were observed. Thirty-two animals were collected the night of March 6 after a 3.8 inch rainfall when the water temperature was 10°

C. No animals were observed the next night when the air temperature had dropped to 7° C. and the water temperature to 5°.

The day time retreats were at first supposed to be in the lagoon or the deeper ditches. It was assumed that during the flooding rains the animals moved from the deeper water areas into the shallow pools and ditches in search of food. Repeated observation of animals in isolated shallow pools forced an early discard of this hypothesis. The animals live in underground burrows below all the lower sections of the golf course where rains will form temporary pools that will permit them to emerge and seek food. It is assumed that they remain near the water table, moving up and down in the burrows as is necessary.

As these salamanders have no gills and must reach the water surface to respire, one would expect to find some animals in the water after a flooding rain during the day. Seven were observed out of their burrows during the day when the pools were flooded. All were actively seeking shelter. It is assumed that these were forced to move from deep burrows to those with access to the surface.

It is not known whether they can construct deep burrows or not but they have been observed to push their way into the soft mud and debris of the bottom. The golf course has large numbers of crawfish burrows so that the underground existence of the *Amphiuma* does not require burrowing ability.

When the water levels are low, the animals remain in their burrows. When rains flood the area, they move out into the shallow ditches and pools to feed and breed. Rainfall is then the primary factor regulating the movements, growth and breeding cycle of this population. Temperatures are of minor significance as minimum effective temperatures are reached only occasionally during winter and the maximum effective temperature is never reached in underground water or the recently-fallen rain.

DISTRIBUTION IN THE STUDY AREA

Some animals have been taken from almost every small pool and drainage ditch in the park but definite concentrations occur. Three areas have consistently yielded animals when examined after a flooding rain. A shallow, bowl-like depression (1, A, figure 1) just adjacent to the northern end of the lagoon accumulates as much as 10 inches of water that drains into the lagoon until 1 to 3 inches remain. Evaporation and soil drainage rapidly eliminates this. A network of burrows is present in the soft, damp soil beneath this depression and an abundance of *Amphiuma* are sheltered there.

A second pool located in the middle of the golf course (2, C, figure 1) never has more than 3 inches of water accumulated over the closely mown grass. This pool and a shallow ditch draining it to the south are usually occupied by one or more salamanders. The most productive area has been the network of drainage ditches in section E. A point where two of these ditches join (3, E, figure 1) has regularly yielded both small and large individuals.

These three most productive areas are not the lowest spots in the park and are not the first to be flooded. The explanation of the concentrations in these places may rest on an examination of the sub-surface soil.

Some difference has been noted in the distribution of the various sizes in the park. The very large individuals occur in the lagoon or the deep entrances of the drainage ditches emptying into it. Only one large individual, a male in breeding condition, has been collected more than a few yards from the deeper waters. Sexually mature individuals occur throughout the park.

MOVEMENTS

The repeated observation of animals in the same burrow provided a basis for the assumption that the adults did not move far from a home burrow except possibly during the breeding season. Of 22 indi-

viduals collected and released within 15 yards of point 3 in section E in August of 1946 two were collected near the same point in January of 1947 and one 325 yards away in the drainage ditch near the boundary between sections C and E. Of 18 released at point 4, section D, 4 were subsequently recovered from the network of ditches in the southwestern corner of section E and one within 5 yards of the release point. These were dispersed in the ditches. None of the recoveries were found in other sections. These recoveries suggest that these animals can move about the park freely but that they restrict their movements to that area in which food is available.

One animal followed for 2 hours one night moved slowly from a pool (point 2, section C) along a shallow ditch toward section E. Although it moved only 70 feet during this time it captured one crawfish and several small unidentified animals by burrowing in each mass of vegetation it passed and constantly exploring the bottom with its snout.

During heavy rainfall, the *Amphiuma* often move overland. It is not unusual to find them a few inches from the water edge and several have been collected a dozen feet from the nearest water. One large adult male was collected moving across the wet grass 40 feet from the nearest pool of water.

A pursued animal in clear water will swim rapidly along the bottom searching for a place of concealment. If the bottom is soft, they literally melt into it. One downward thrust of the head and a push from the powerful body sinks them into the bottom. A mass of debris will provide similar effective concealment.

The rapidly flowing currents in the shallow ditches after a heavy rain will sometimes sweep small individuals away from their burrows. These have been collected from an accumulation of debris about an entrance to an underground drainage tunnel. Hatchlings are especially susceptible to these currents. The large adults have little difficulty.

COURTSHIP

Courtship activity of a male and two females was observed during the last 10 days of July by Baker, Baker and Cald-

well ('47). The animals swam rapidly about in a spiral fashion occasionally flipping the tail from the water and making sudden dashes toward the bank. The fe-

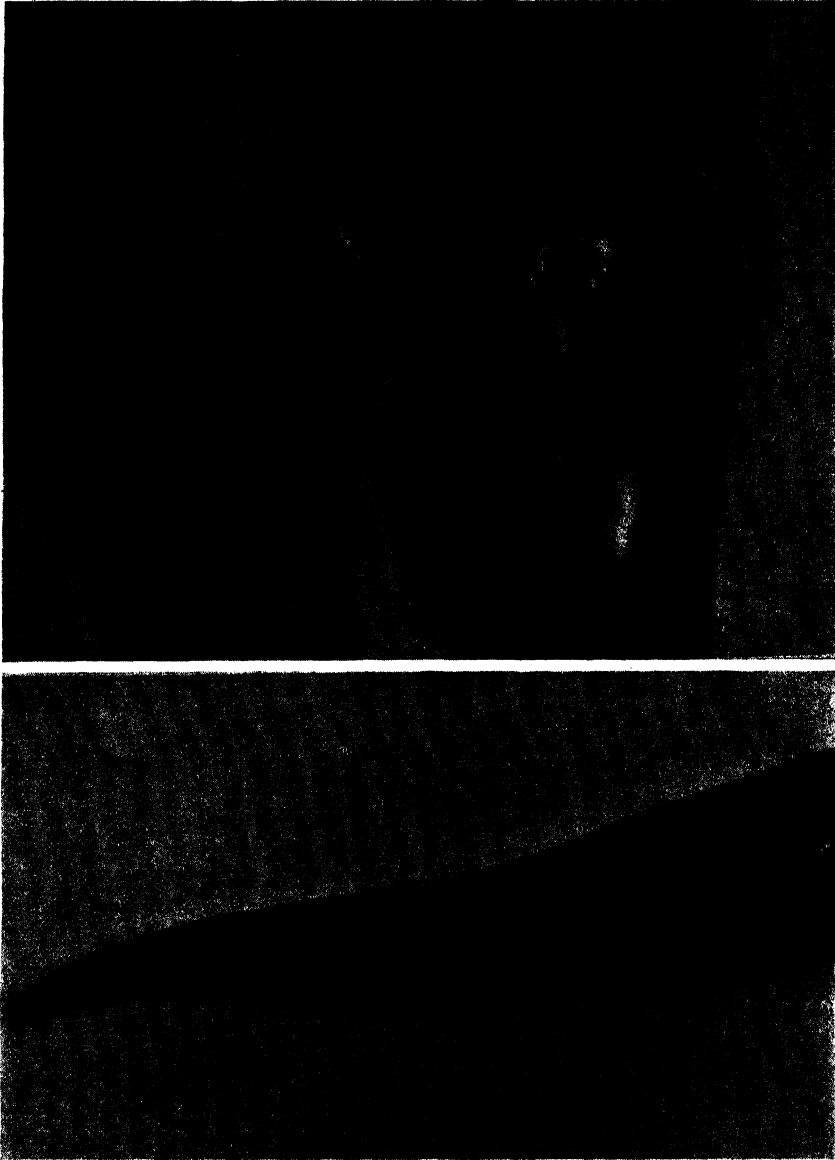


FIG. 5 (upper). The cloaca of a female and a male taken during the courtship season. The cloaca of the male is much swollen and partially everted. The white mass between the cloacal lips is a spermatophore ready for transfer to a female.

FIG. 6 (lower). The tail of a marked salamander. The depression on the dorsal part is banded by a deposit of dark pigment. A notch of twice the depth of the depression was cut into the tail two months previously. The injury is healed but the V shape of the original notch is evident in the specimen.

male was observed to glide under the male and roll over so as to place her cloaca against that of the male. This position was retained for twenty minutes. Dr. F. H. Wilson ('41) states that the cloaca of males from New Orleans reaches maximum development in January, February and March and that copulation takes place during this period.

As the courtship season approaches the cloaca of the male becomes swollen to the extent that it is partially everted and remains so during the entire season (figure 5). Males in this condition were collected in the park on two successive years in the period from mid-January to mid-May. The peak of the male activity is reached in March and by May some males have the cloacae reduced.

A driving rain appears to be a strong stimulus to courtship activity. More than 100 individuals were observed in one shallow pool (1, section A, figure 1) March 25, after a heavy rain. The animals were unusually active and swimming rapidly through the water with the tails often flipping above the water surface. Others were observed crawling about on the wet leaves and grass several feet from the waters edge. Of 32 collected, 6 were lying adjacent to each other but it could not be determined whether or not the cloacae were in contact. All the males had the typical swollen cloacae and all the 12 large females examined contained sperm. Each male had one or more lacerations of the body from bites. Some of these were two millimeters in depth. One male had more than 20 well defined teeth prints and cuts on its body.

Males badly scarred from bites were collected during the period January to April. These bites rarely cause serious injury but occasionally interfere with movement to the extent that the animal cannot seek shelter. Five such living but lacerated males have been collected from the ditches during the day.

The courting male retains a flake of sperm cells between the cloacal lips (figure 5). This spermatophore is a flattened,

irregular in outline, mass of sperm bound together with a gelatinous secretion. These spermatophores have been found in the cloacal lips of 13 females. The sperm flake is thus transferred intact to the female cloaca. Kreeger ('42) has demonstrated the presence of dorsal and ventral spermatheca in the female and reported that sperm may be retained for 7 to 8 months.

EGG-LAYING

The eggs of *Amphiuma* have been found in August in Arkansas (Hay '88), in August, September and mid-winter in Tennessee (Parker, '37), and in February in Florida (Weber, '44). The date of deposition was not known for any of these broods. It is probable that the young remain in the eggs until they are flooded by water. Weber ('44) has suggested that this may be true for *Amphiuma means*. If true, this would partially explain the wide variation of dates on which field-collected nests are reported.

Of 37 individuals collected during a heavy rain June 25, 1946, 4 were mature females containing eggs ready for deposition. One of these had several eggs projecting from the cloaca when it was captured. Retained in the laboratory it was not observed to deposit the eggs but dissection indicated that they had been deposited and subsequently eaten. The oviducts were empty and the stomach filled with eggs.

A string of eight eggs was found coiled around a plant stem in a shallow ditch of rapidly flowing water on the same date (figure 8). The eggs did not develop when retained in the laboratory. These, the only eggs observed in the park, may have been washed from a burrow and swept into the ditch by the rapidly moving water. Certainly they are not normally deposited in the open.

The ditches of the park have been cleared of all large plants, logs and debris so that the *Amphiuma* can find shelter only in burrows. The absence of eggs in the ditches or pools during the egg-laying

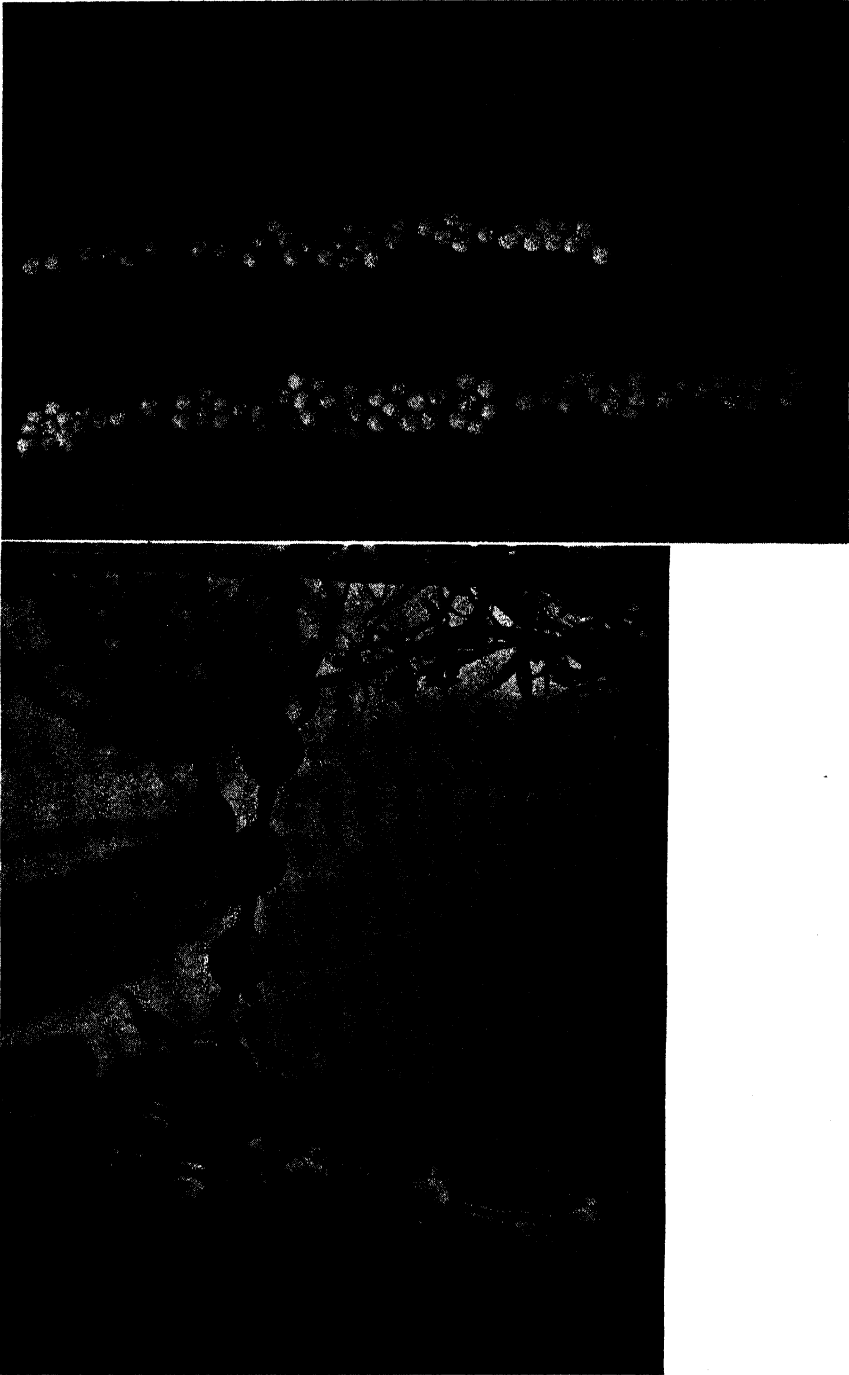


FIG. 7 (upper). The ovaries of three females of the same body length collected on the same date. The upper ovary will not produce eggs during the next egg-laying season; the lower ovaries will.

FIG. 8 (lower). An egg string of *Amphiuma* found in a shallow ditch.

season and the repeated collecting of recently hatched young from shallow, isolated, temporary pools indicates that the eggs are laid in burrows. Mr. A. H. Chaney and Mrs. Jane Spauschus collected a total of 18 hatchlings retaining gill vestiges from a small isolated pool on different nights. These were burrowing among the grass roots and between the grass blades. A single burrow led from the pool. It is assumed that a clutch of eggs had hatched in the burrow and that these young moved to the surface to feed when the burrow was flooded.

A female collected September 28 had a string of egg cases in her stomach. The eggs were not present and it could not be determined whether they had been digested or the animal had swallowed an empty string of cases.

Females with follicles near the size of ovulation (5-7 mm.) were found only during the months of May and June. The smallest female containing such follicles measured 33 cm. in body length. None of the females smaller than this contained any enlarged follicles and only 42% of those larger than 33 cm. contained an enlarged group (fig. 7). Wilson ('42) observed that only 50% of the large females taken in Audubon Park contained eggs sufficiently large for deposition during the next season and has suggested that a two year reproductive cycle is indicated. These data substantiate Wilson's observations. This two year ovarian cycle may not be characteristic of those individuals occupying a habitat where food is constantly available and activity is not controlled by rainfall.

The number of eggs varied from 42 to 131, mean 98, in 26 females. The size of the follicles progressively increases from August to May. The range in September was 1.5-2.2 mm.; in October 1.2-3.0 mm.; in January 2.5-3.0 mm.; in March 3.5-4.5 mm.; in May 5-6 mm.

GROWTH

None of the recovered individuals provided growth data. The toe marks were

questionable and only the group mark (tail scar) could be positively identified (figure 6). The monthly samples, however, furnish some information on growth.

The smallest young were collected in November. A sample of 22 ranged in body length from 44 to 62 mm., mean 50.2 mm. (figure 4). This group included the smallest individuals collected. None with a body length of less than 60 mm. were collected in other months. The smaller individuals had gill vestiges; the maximum gill filament being .4 mm. in length. Baker ('45) describes a group of eggs shipped from New Orleans to the University of Michigan in November. Some of the eggs hatched in transit. The writer was present when the eggs were received at the University of Michigan and had an opportunity to observe the eggs during the hatching period. Most of the eggs hatched over a period of 5 days. No measurements were taken at the time but Dr. Norman Hartweg, Curator of the Herpetological Collections in the University of Michigan Museum of Zoology, loaned some of the eggs and young for examination. Of four young measured the body length ranged from 43-51 mm. A fifth one, dissected from an egg, measured 46 mm. in length. A comparison of these with the November collected sample from Audubon Park permits only the assumptions that the park sample contains recently hatched young or individuals that had been hatched for some time and had not grown.

Other hatchlings were collected in March, April and May. A progressive increase in mean body length (figure 4) is demonstrated when the lengths are plotted by date. The resulting growth curve has only a slight slope from November to March. It is probable that growth is slower than the slope suggests during the months of November to January and more rapid than indicated in February. The growth rate is rapidly increased in March, April and May. If this growth rate continues throughout the warmer months, females might be expected to

reach the size of sexual maturity relatively slowly. If it may be assumed that growth proceeds at this rate (6 mm. per month) during 9 months of the year, the female would require more than 4 years to reach sexual maturity.

FEEDING HABITS

The *Amphiuma* apparently detect their food by either its movement or odor. A rapid forward or lateral strike then captures the prey. If the prey moves away the *Amphiuma* will follow slowly until within striking distance. If resistance is encountered, the body is twisted violently and rotated rapidly in the water until the resistance is conquered. Captive animals used this motion to twist and tear sections from a large fragment of meat placed in an aquarium. Trot line leaders are twisted into tight spirals by a hooked animal.

The food habits of the *Amphiuma* have been investigated by A. H. Chaney, a graduate student at Tulane University, who reports that the principal items in the diet are crawfish, earthworms and insects. Tadpoles and small fishes are sometimes captured (Chaney, '48).

DISCUSSION

The abundance of these large salamanders in the vicinity of New Orleans may be attributed to the loose soil permitting easy burrowing, the high water table and the availability of food. The animals have a high reproductive potential and few natural enemies. Large populations may develop rapidly. The precise role of these populations in a community remains unknown.

Much of the life history is in need of further exploration. The spermatophores, courtship, egg-laying, feeding habits need further description. The two-year reproductive cycle and its relation to food-availability, the growth rate, and longevity require additional investigation. Data on population density, movements, burrowing habits, ability to aestivate are essential before we have any substantial

understanding of the population dynamics of this form.

SUMMARY

The salamander, *Amphiuma tridactylum* Cuvier, is abundant on the golf course of the Audubon Park, New Orleans. The animals remain in underground burrows, apparently moving up and down with the fluctuating water table, until rains cause much of the park to be flooded with several inches of water. During such periods the *Amphiuma* leave the burrows to seek food in the shallow pools and ditches. The activity of the animals is thus regulated by the rainfall.

When water is present in the ditches and lower areas daily activity reaches its peak between 10 and 12 p.m. After this time most of the animals retreat to burrows. They are active throughout the year except when the water temperature is below 9° C.

None of the individuals of the Audubon Park population reach as large a size as individuals collected from surrounding areas. The females have a two-year reproductive cycle. The failure to attain maximum size and the long ovarian cycle may be a result of the limitation on activity imposed by the habitat, only a flooding rain permitting feeding.

The males are reproductively active from mid-January to mid-May. A driving rain appears to be a direct stimulus to courtship. A sperm flake is transferred to the female cloaca by contact. The female deposits 42 to 131 eggs in the burrows during May or June. The young remain in the burrow, emerging only when the elevation of the water table forces them upward. They measure 43–51 mm. in body length when hatched and may reach a body length of 10–14 cm. in their first year. The females become sexually mature when they reach a body length of 33 cm.

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PALYNOLOGICAL STUDIES AT SODON LAKE, MICHIGAN
PART III. THE SEQUENCE OF POLLEN
SPECTRA, PROFILE I

STANLEY A. CAIN AND J. V. SLATER

Cranbrook Institute of Science, Bloomfield Hills, Michigan

In a stratigraphic study of the sediments in and about Sodon Lake, Oakland County, Michigan, Cain and Slater (Ms.) examined 10 profiles from a transect line tangent at its mid point to the lake shore and about 20 feet from the water's edge at the closest (mid) point. A boring made at this point is designated Profile I; the materials of this boring were selected for pollen analysis. An additional transect of four profiles lies along a radius of the lake and intersects the former transect at right angles at the site of Profile I.

The boring tool (modified Hillier peat sampler) was so calibrated that samples were obtained in pairs separated by 6-inch intervals, each sample being obtained about 3 inches distant from the respective ends of the opening of the tool. Each sample consisted of 5-10 cc. of sediment, and was placed immediately into a plastic vial. The vials were stored in a refrigerator until slides could be prepared for pollen analysis by the Erdtman acetolysis method, modified by use of fresh rather than dried material. The samples were then dried for purposes of standard color description and other types of analysis, Cain and Slater (Ms.).

The profiles were located on the west side of the lake where they transected certain aquatic zones, herbaceous and shrub fens, and various types of swamp forest. The present-day vegetation of the lake has been described by Cain and Slater ('48). As would be expected from the position of Profile I, in the present-day herb-shrub fen, the first several feet of the sediments were composed of sub-aerial peat. At the 8-ft. level the sediments changed predominantly to marl, which was continued to the 23-ft. level except for two interruptions. Starting at

14 feet, there was a peat layer of about 9 inches thickness. Just above the 21-ft. level was a second, but thinner, peat layer. Below the marl, between 23 and 23.5 feet was a sandy layer, under which was a slightly bluish clay layer of which we could obtain only a 6-in. sample. Since our tool was incapable of penetrating any deeper into these stiff sediments, the column has a total thickness of 24 feet, and is analyzed on a basis of samples from 6-in. levels.

Two slides of the acetolyzed material were prepared for each level. This was usually a superabundance of material, but in some cases additional slides were prepared so as to obtain adequate numbers of pollen grains. At a few levels we were unable to obtain as many as 200 pollen grains of trees, although the total number employed in the spectra was never less than 146 and the average was well over 200 grains. At two levels (1.5 and 2.5 feet) the peat apparently does not contain many microfossils, for repeated attempts failed to yield any pollen. The material was saffranin stained and mounted in glycerine jelly. Examination was made at a magnification of 440 \times with a compound binocular scope and a mechanical stage. After the 49 spectra had been computed, the slides were re-examined for size-frequency studies of spruce (Cain, '48) and pine pollen (Cain and Cain, '48), and for non-tree pollen and spores such as *Sphagnum*, *Nuphar*, grasses, sedges, *Lycopodium*, etc.

Since the identification of pollen grains and their proportions in the various spectra are so critical for the interpretation of vegetational and climatic history by pollen analysis, one always wonders about the reliability of particular results. Some

interesting information on that point is given in table I. In certain instances each of the authors independently prepared duplicate spectra as checks. In other cases second spectra were prepared to verify certain abrupt changes in the representation of certain pollen types. Five sets of these data show a remarkable uniformity of results. In no case are the differences sufficient to alter any interpretations of the data.

Due to our complete lack of quantitative information on over- and under-representation by pollen grains of certain types, and due to the fact that successive samples taken at 6-in. intervals tend to show more or less strong fluctuations, the particular percentage value of a pollen type in a spectrum has only a general significance. Confidence in pollen analytic interpretations of vegetational and climatic history is based not on actual values but on (1) presence and absence—where grains of a certain type first appear or finally disappear in a column, and (2) on well-marked trends. Finally, (3) even the trends can be considered only apparent unless they are substantiated and corroborated by similar trends reoccurring from many borings of different sediments over a considerable area or region. That is to say, the strongest case for pollen analysis rests on the establishment of

regional pollen profile patterns or types. The Sodon Lake profile, then, becomes simply one more case in the gradual accumulation of regional data. An effort will be made to fit it into the regional picture as far as it is developed at the present time.

One further effort was made to complete the picture presented by the present series of spectra. The slides were re-studied in toto for any level where a particular type of grain found elsewhere had not entered into the spectrum. If it was not found at all, absence is indicated by a dash in table II and the other tables. If it was found to be present, even by one grain, it is indicated as present (P). Note that the percentages are based upon identifications of a limited number of grains (usually more than 200), but that the symbols (—) and (P) are based upon the examination of the whole mounted material, often a few thousand grains. We were thus able to extend the upper limits for *Abies* and *Picea* and the lower limits for *Tsuga*, and fill in several of the gaps for many of the types of grains.

DISCUSSION OF PROFILE I

Auer ('30), studying southeastern Canadian bogs, and Sears ('31), on a basis of one bog studied in Ohio, found a suggestion of two post-glacial periods of ret-

TABLE I. Independent duplicate spectra (percentages) for certain samples, Profile I, Sodon Lake

| Depth below surface in feet | <i>Abies</i> | <i>Picea</i> | <i>Pinus</i> | <i>Quercus</i> | <i>Carya</i> | <i>Betula</i> | <i>Fagus</i> | <i>Acer</i> | <i>Tilia</i> | <i>Tsuga</i> | <i>Nyssa</i> | <i>Ulmus</i> | <i>Juglans</i> | <i>Carpinoid</i> | Undetermined | Total number of pollen grains |
|-----------------------------|--------------|--------------|--------------|----------------|--------------|---------------|--------------|-------------|--------------|--------------|--------------|--------------|----------------|------------------|--------------|-------------------------------|
| 15.5 | 0.3 | 0.3 | 5.0 | 71.2 | 4.0 | 0.7 | 2.3 | 1.7 | 1.7 | 1.7 | — | 6.3 | 1.3 | 2.0 | 2.0 | 302 |
| | — | — | 6.7 | 67.2 | 6.7 | 1.3 | 5.9 | 1.7 | 3.8 | — | 0.4 | 5.1 | — | 0.8 | 0.4 | 238 |
| 16.5 | — | 0.5 | 4.1 | 70.5 | 1.4 | — | 3.2 | 2.3 | 0.5 | 0.5 | 0.5 | 10.6 | 1.4 | — | — | 217 |
| | — | — | 5.8 | 71.3 | 2.9 | 0.4 | 3.4 | 2.5 | 2.9 | — | 0.4 | 4.2 | — | 2.9 | 2.6 | 234 |
| 20.0 | — | P | 4.8 | 74.6 | 1.8 | 2.2 | — | 4.4 | 0.4 | — | — | 6.1 | — | 2.2 | 3.1 | 228 |
| | — | 0.4 | 5.9 | 77.5 | 3.4 | 2.9 | 2.1 | 3.7 | 0.4 | — | — | 1.8 | — | 2.1 | 2.1 | 241 |
| 21.5 | 0.5 | — | 55.9 | 25.7 | 1.5 | 4.4 | 0.5 | 4.0 | — | — | — | 4.9 | — | 1.5 | 1.0 | 202 |
| | 0.4 | 0.9 | 55.2 | 33.5 | 0.9 | 3.5 | 1.3 | 1.7 | 0.4 | — | — | 0.4 | — | — | 1.7 | 230 |
| 22.5 | 0.8 | 1.3 | 41.5 | 33.1 | 1.7 | 3.9 | — | 0.4 | — | — | — | 3.7 | — | 11.7 | 1.3 | 239 |
| | — | P | 43.5 | 34.9 | 3.0 | 3.4 | 0.4 | 1.2 | — | — | — | 2.0 | — | 6.9 | 3.4 | 232 |

— = absent.

P = present, at least one grain found.

regression of reversal of the general successional trend toward mesophytism. These are considered periods in which the climate was drier and possibly warmer. Later, when numerous profiles were available, Sears ('35, '38) recognized that

TABLE II. Pollen spectra (percentages) of Profile I, Sodon Lake

| Depth below surface in feet | Number of grains used in spectra % | Tree pollen spectra | | | | | | | | | | | | | | |
|--------------------------------|---------------------------------------|---------------------|----------------------|--------------------|---------------------|-----------------------|----------------------|---------------------|--------------------|------------------------|-----------------------|-------------------|-------------------|------------------------|----------------|--------------------------------|
| | | <i>Abies</i> —fir | <i>Picea</i> —spruce | <i>Pinus</i> —pine | <i>Quercus</i> —oak | <i>Carya</i> —hickory | <i>Betula</i> —birch | <i>Fagus</i> —beech | <i>Acer</i> —maple | <i>Tilia</i> —basewood | <i>Tsuga</i> —hemlock | <i>Nyssa</i> —gum | <i>Ulmus</i> —elm | <i>Juglans</i> —walnut | Carpinoid type | Undetermined or undeterminable |
| 0.1 | 200 | — | — | 3.5 | 85.0 | 3.5 | 1.5 | P | 1.0 | 0.5 | 3.0 | — | 1.5 | 0.5 | — | — |
| 0.5 | 240 | — | — | 5.0 | 85.8 | 2.5 | 0.4 | 1.7 | 2.1 | — | 1.2 | — | 0.8 | — | — | 0.4 |
| 1.0 | 218 | — | — | 4.6 | 74.3 | 4.1 | 0.9 | 0.5 | 1.1 | 1.3 | — | — | 6.4 | 2.9 | 1.8 | 3.7 |
| 1.5 | * | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 2.0 | 200 | — | — | 7.0 | 70.0 | 10.0 | 1.0 | 0.5 | 1.5 | 2.0 | — | — | 2.0 | 2.0 | 2.5 | 1.5 |
| 2.5 | * | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 3.0 | 170 | — | — | 6.5 | 77.0 | 4.1 | 0.6 | 0.6 | 2.9 | 1.2 | — | 1.2 | 2.4 | 0.6 | 0.6 | 2.4 |
| 3.5 | 237 | — | — | 0.8 | 84.3 | 3.3 | 1.2 | 1.6 | 1.2 | 1.2 | — | — | 3.7 | 0.4 | 0.4 | 1.2 |
| 4.0 | 209 | — | — | 2.9 | 87.1 | 1.3 | 0.4 | 0.4 | 0.8 | 0.4 | — | — | 2.9 | — | 0.8 | 2.4 |
| 4.5 | 191 | — | — | P | 86.8 | 2.6 | P | 1.5 | 1.5 | — | — | 0.5 | 4.7 | — | 0.5 | 1.5 |
| 5.0 | 254 | — | — | 2.8 | 81.1 | 3.9 | 0.8 | 2.8 | 1.9 | P | 1.2 | — | 2.4 | 0.4 | 0.8 | 1.9 |
| 5.5 | 217 | — | — | 9.2 | 82.0 | 2.3 | P | 0.5 | 2.8 | 0.8 | — | — | 0.5 | — | 0.5 | 0.5 |
| 6.0 | 239 | — | — | 4.6 | 79.1 | 6.2 | — | 0.8 | 0.8 | P | 0.4 | — | 2.8 | 0.8 | 0.4 | 3.8 |
| 6.5 | 179 | — | — | 8.9 | 67.5 | 4.4 | 0.5 | 0.5 | — | 2.8 | 1.1 | 0.5 | 1.7 | — | 7.2 | 4.4 |
| 7.0 | 228 | — | P | 12.3 | 76.7 | 4.8 | — | 0.4 | 1.8 | 0.4 | 0.4 | — | 1.3 | — | 1.7 | — |
| 7.5 | 146 | — | — | 14.3 | 67.2 | 4.8 | 1.4 | 2.7 | — | P | P | — | 4.8 | 1.4 | 2.1 | 1.4 |
| 7.6-7.8 | 237 | — | P | 13.9 | 59.5 | 8.0 | 0.8 | 2.1 | 1.3 | 2.9 | 0.8 | — | 3.3 | 2.1 | 2.1 | 2.9 |
| 8.0 | 279 | — | — | 5.0 | 75.6 | 5.3 | 0.4 | 2.2 | 2.2 | 2.9 | 0.4 | 0.4 | 1.4 | 1.4 | 0.8 | 2.2 |
| 8.5 | 284 | — | — | 5.9 | 71.1 | 2.5 | 1.1 | 4.5 | 1.1 | 2.8 | 0.4 | — | 3.9 | 1.8 | 3.2 | 1.8 |
| 9.0 | 278 | — | — | 5.8 | 72.7 | 2.5 | 0.4 | 3.6 | 0.7 | 1.1 | 0.4 | — | 5.4 | 2.2 | 2.9 | 2.5 |
| 9.5 | 250 | — | — | 5.2 | 71.2 | 3.2 | 0.8 | 2.8 | 2.4 | 0.4 | 1.2 | 0.4 | 5.2 | 1.6 | 2.0 | 3.6 |
| 10.0 | 324 | — | — | 5.6 | 71.6 | 2.8 | 0.6 | 6.5 | 4.3 | P | P | 1.2 | 4.6 | 0.9 | 0.3 | 1.9 |
| 10.5 | 401 | — | — | 2.0 | 78.5 | 3.8 | 0.8 | 2.7 | 2.3 | 1.2 | 0.8 | 0.3 | 4.7 | 1.7 | 1.5 | 0.8 |
| 11.0 | 343 | — | — | 5.2 | 67.5 | 6.9 | 0.8 | 3.3 | 2.8 | 1.7 | 0.8 | 0.8 | 6.3 | — | 1.4 | 2.4 |
| 11.5 | 271 | — | — | 6.6 | 69.7 | 6.3 | 0.7 | 1.1 | 4.8 | 0.7 | 1.4 | — | 4.4 | — | 0.4 | 3.7 |
| 12.0 | 249 | — | P | 2.8 | 71.5 | 2.4 | 1.2 | 0.4 | 2.8 | 1.2 | 2.8 | — | 6.8 | — | 1.6 | 2.8 |
| 12.5 | 277 | — | — | 7.9 | 72.9 | 6.8 | P | 1.8 | 1.1 | 0.7 | 0.4 | — | 5.8 | — | — | 2.5 |
| 13.0 | 267 | — | — | 3.7 | 76.0 | 3.7 | 0.4 | 1.9 | 1.4 | 4.2 | P | — | 4.6 | — | 0.8 | 2.6 |
| 13.5 | 228 | — | — | 4.3 | 68.9 | 1.3 | 3.9 | 3.1 | 1.8 | 5.3 | 0.4 | 0.4 | 6.6 | — | 1.3 | 2.6 |
| 14.0 | 251 | — | — | 1.9 | 70.9 | 9.9 | 0.8 | 0.8 | 0.8 | 4.7 | P | P | 3.6 | 2.8 | 0.8 | 2.8 |
| 14.5 | 219 | — | P | 9.7 | 70.7 | 4.6 | 1.4 | 4.1 | 1.4 | 2.3 | P | — | 3.7 | — | 0.9 | 2.3 |
| 15.0 | 260 | — | P | 6.2 | 65.3 | 9.6 | 1.5 | 3.8 | 1.9 | 3.8 | — | — | 5.3 | — | 0.7 | 1.5 |
| 15.5 | 302 | — | 0.3 | 5.0 | 71.2 | 4.0 | 0.7 | 2.3 | 1.7 | 1.7 | 1.7 | — | 6.3 | 1.3 | 2.0 | 2.0 |
| 16.0 | 250 | — | — | 8.4 | 70.4 | 1.6 | 1.6 | 1.2 | 1.2 | 4.4 | 0.4 | 1.2 | 6.0 | — | 2.0 | 1.6 |
| 16.5 | 217 | — | 0.5 | 4.1 | 70.5 | 1.4 | P | 3.2 | 2.3 | 0.5 | 0.5 | 0.5 | 10.6 | 1.4 | — | — |
| 17.0 | 278 | — | P | 6.1 | 68.3 | 6.1 | 1.3 | 5.4 | 1.3 | 1.1 | 0.4 | — | 5.1 | — | 1.8 | 2.9 |
| 17.5 | 230 | — | — | 7.3 | 73.9 | 3.1 | 1.7 | 2.6 | 1.7 | 2.2 | P | — | 2.6 | — | 2.6 | 2.2 |
| 18.0 | 195 | — | — | 6.7 | 58.4 | 6.1 | 4.6 | 6.1 | 2.1 | 4.1 | 0.5 | 0.5 | 7.1 | — | — | 3.1 |
| 18.5 | 208 | — | P | 19.7 | 49.0 | 6.2 | 3.8 | 3.8 | 5.8 | P | 0.5 | 0.5 | 5.3 | — | 1.9 | 3.4 |
| 19.0 | 209 | — | P | 14.4 | 55.5 | 5.7 | 4.3 | 0.9 | 11.0 | 0.5 | P | 0.9 | 2.8 | — | 0.9 | 2.8 |
| 19.5 | 240 | — | P | 21.7 | 47.9 | 4.2 | 6.6 | 0.8 | 8.7 | 0.8 | — | — | 3.3 | — | 2.1 | 3.7 |
| 20.0 | 228 | — | P | 4.8 | 74.6 | 1.8 | 2.2 | — | 4.4 | 0.4 | — | — | 6.1 | — | 2.2 | 3.1 |
| 20.5 | 200 | — | — | 39.0 | 34.0 | P | 9.5 | 0.5 | 7.5 | — | — | — | 5.5 | — | 1.0 | 3.0 |
| 20.7 | 273 | P | P | 25.6 | 49.5 | 2.5 | 5.1 | 0.7 | 5.9 | 0.7 | — | — | 7.3 | — | 1.1 | 1.4 |
| 21.0 | 230 | P | P | 52.2 | 30.4 | 1.3 | 6.1 | — | 3.0 | — | — | — | 3.9 | — | 2.2 | 0.8 |
| 21.5 | 230 | 0.5 | 0.9 | 55.2 | 33.5 | 0.9 | 3.5 | 1.3 | 1.7 | 0.4 | — | — | 0.4 | — | — | 1.7 |
| 22.0 | 483 | — | — | 12.7 | 58.8 | 1.6 | 6.6 | 0.2 | 4.5 | 0.6 | — | — | 5.8 | — | 5.6 | 3.5 |
| 22.5 | 239 | 0.8 | 1.3 | 41.5 | 33.1 | 1.7 | 3.9 | — | 0.4 | P | — | — | 3.9 | — | 11.7 | 1.3 |
| 23.0 | 244 | P | 5.0 | 80.7 | 5.3 | 0.2 | 3.4 | 0.2 | — | P | — | — | 2.6 | — | 1.6 | — |
| 23.5 | 180 | — | 3.9 | 28.3 | 45.5 | 1.7 | 7.2 | 2.2 | 1.1 | 0.6 | — | — | — | — | 5.6 | 3.9 |
| 24.0 | 322 | 1.5 | 85.7 | 4.0 | 5.6 | 0.6 | 1.5 | — | 0.9 | — | — | — | — | — | — | — |

— = absent.

* = no satisfactory preparations obtained.

P = present, at least one grain found.

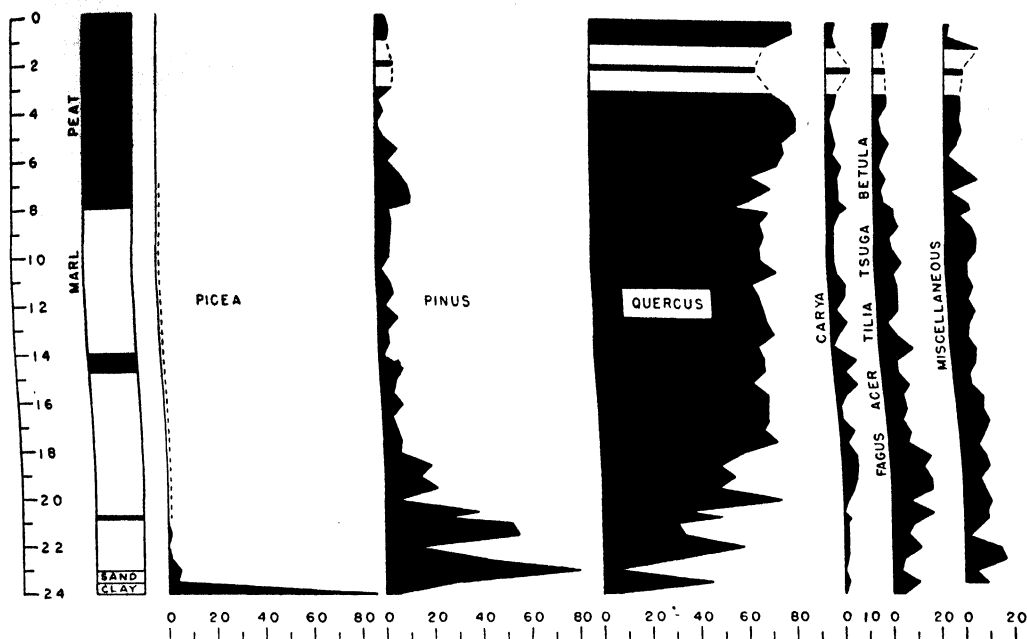


FIG. 1. Pollen diagram showing percentage occurrence of important groups of pollen grains at six-inch levels.

there was a Central Deciduous type of pollen profile distinct from a Northern Lake Forest type and a Northeastern Oceanic type. In a very schematic manner, the Central Deciduous type of the North Central States starts with a complete dominance of *Picea-Abies* pollen. This is followed by a more or less strong development of *Pinus*; then deciduous species, *Quercus* predominating, hold the dominance for the last two-thirds of the profile. The central part of this period often shows a rise of grasses and more xerophytic deciduous tree species. Later Sears ('42a, '42b) formalized his examination of over one hundred available profiles in a division of them into five periods representing times of floristic and climatic differences. Smith ('40) gave his opinion as to the significance of the available profiles for late-glacial and post-glacial history, and suggested their correlation with the commonly recognized periods of European workers. Potter ('47) employed Sears' periods in a study of several northern Ohio profiles. In the following paragraphs an attempt is made

to examine the Sodon Lake profile, figures 1 and 2, in the light of these concepts.

Period I

This is a time of cool moist climate and of dominance by *Abies* and *Picea* pollen in the spectra. It is considered a pre-boreal period, with the *Picea* maximum coincident with the last abrupt expansion of ice sheets, possibly 8-10,000 B.C. (Antevs, '39). In the Central Deciduous region *Abies* pollen is usually not strongly represented. Northward there is often an *Abies* maximum before the *Picea* maximum. Sears ('42a) considers the shift from *Abies* to *Picea*, and in Period II, to *Pinus*, as a lowering of the degree of mesophytism, for the usual order of succession is from *Pinus* to *Abies* and *Picea*. Potter claims that both genera indicate a cold wet climate (annual temperature not over 40° F., precipitation not less than 25 in.), but with *Picea* extending farther northward and in general having a slightly broader tolerance than *Abies*.

The Sodon Lake profile penetrates below the marl sedimentation into a sandy

layer (23–23.5 feet) and a clay layer (23.5–24 feet). Strong *Picea* representation occurs only in the deepest spectrum, and that constitutes our only record of the pre-boreal Period I. The broad-leaf genera: *Quercus*, *Carya*, *Betula* and *Acer* are already represented in small amounts. In Ohio and Indiana *Quercus* generally follows *Picea-Abies*, but in bogs in Illinois, Wisconsin, and Minnesota (Voss, '34), it is present with the early conifers.

Period II

This is the period of *Pinus* maximum that is considered to be drier and probably warmer than Period I. It is the earliest post-glacial period and the beginning of boreal time. Some profiles from the Central Deciduous area of the North Central States show a rise of *Quercus* concomitant

with the *Pinus*. The Sodon Lake profile shows a minimum of *Quercus* coincident with the maximum of *Pinus*. Sears ('42b) considers that the dryness may have been relative, due to a rise in temperature rather than a lowering of precipitation. This can be inferred from the known northward retreat of *Abies* and *Picea* at this time.

At Sodon Lake the *Pinus* maximum is at 23 feet. Thereafter it shows an oscillating diminution to about 18 feet, where it reaches its average level of composition in the spectra which it maintains to the surface.

Period I–II transition

Smith, Potter, and others have pointed out oscillations in the late pre-boreal, or transition from I to II, between the *Picea*

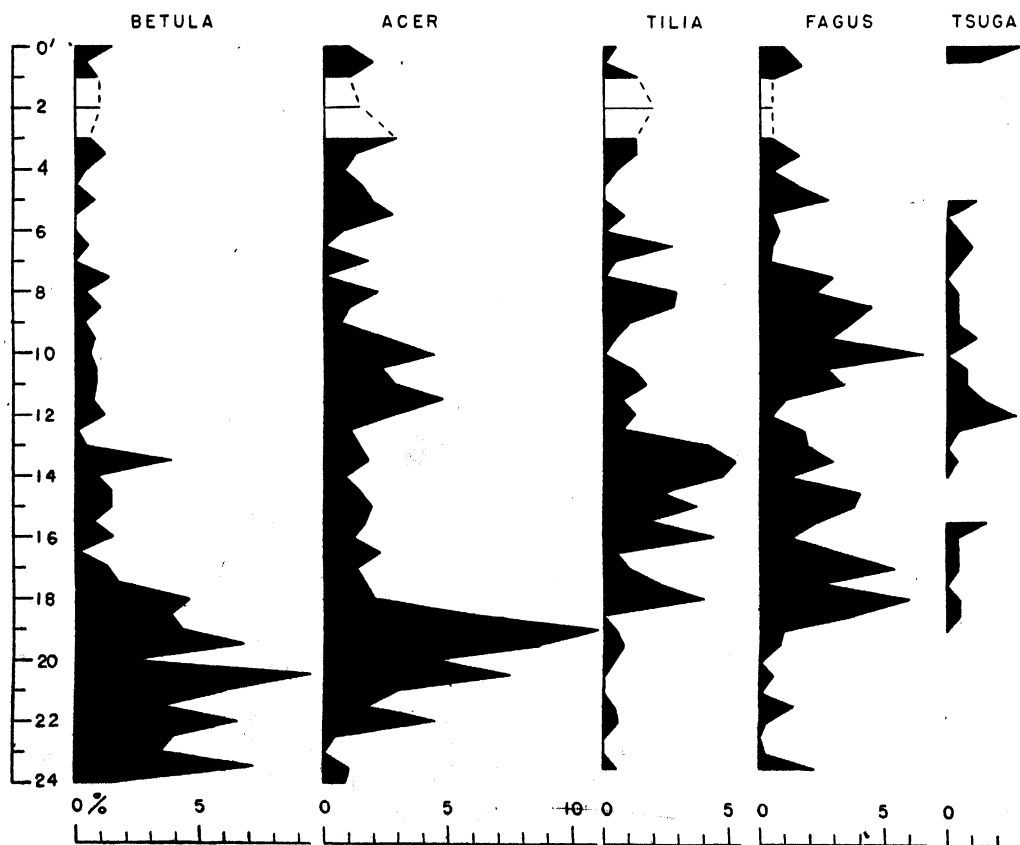


FIG. 2. Pollen diagram showing percentage occurrence of important broadleaf mesophytic genera at six-inch levels. These genera are treated collectively in figure 1.

and *Pinus maxima*. Where *Abies* is important, this often results in a secondary maximum for *Abies*, but more generally there is a temporary increase in deciduous-tree pollen. The late pre-boreal condition is indicated at the 23.5-ft. level at Sodon, as shown in table III, with *Quercus*, *Betula*, *Acer*, *Tilia*, and *Fagus* pollen more abundant than they are in the sediments six inches below or above.

TABLE III. The late pre-boreal transition between Periods I and II

| Genus | Pollen percentages | | |
|----------------|------------------------|------------|---------------------|
| | Period I Pre-boreal | Transition | Period II Boreal |
| | 24 ft. | 23.5 ft. | 23 ft. |
| <i>Picea</i> | 85.7 | 3.9 | 5.0 |
| <i>Quercus</i> | 5.6 | 45.5 | 5.3 |
| <i>Betula</i> | 1.5 | 7.2 | 3.4 |
| <i>Acer</i> | 0.9 | 1.1 | — |
| <i>Tilia</i> | — | 0.6 | P |
| <i>Fagus</i> | — | 2.2 | 0.2 |
| <i>Pinus</i> | 4.0 | 28.3 | 80.7 |

— = absent.

P = present, at least one grain found.

All the students of palynology have realized that only the broadest painting of glacial and post-glacial history can be accomplished when identifications of pollen grains can be carried only to the genus. To do more, however, is difficult if not at times impossible. In other papers of this series the probable species of *Picea* and of *Pinus* are considered, and further ecological considerations are more appropriate there than here.

Period III

This period is considered to be more humid than Period II, and probably also warmer. Among many profiles there is an agreement over hundreds of miles based on increases of species requiring greater humidity for good growth. This is the beginning of the Atlantic period as recognized by European workers. In the North Central States it is usually marked by a maximum of *Fagus* and often of *Tsuga*.

Smith ('40) states that *Betula* increases during the rise of *Pinus* and decreases at the *Pinus* maximum. This occurs at Sodon, but then there is a "recovery" with the absolute *Betula* maximum at 20.5 feet. *Betula* averages about 5 per cent from 23.5–18 feet. Potter ('47) notes the early appearance and development of Betulaceae after *Pinus*. *Acer* commences to increase immediately after the *Pinus* maximum and reaches its maximum at 19 feet. *Tilia* is present with *Betula* and *Acer* but increases only as they decline, reaching peaks of 4 and 5 per cent between 13- and 18-ft. levels. *Fagus*, which is an indicator of the Atlantic period, according to the authors already quoted, begins its increase at 19 feet, developing maxima at 17–18 feet. During the Atlantic period *Fagus* spreads westward of its present limits to Illinois, Wisconsin and Iowa. Fluctuating in amount, it diminishes upward to a low at 12 feet. There is a second "*Fagus* period" between 7.5 and 11 feet. Sears ('42a) found that about half of the profiles that extended to the present show this second development of *Fagus* "followed by a third retrogression." The increase of *Tsuga*, usually together with the rise of *Fagus*, indicates the onset of the Atlantic Period III. At Sodon, *Tsuga* appears first at 19 feet, drops out at 15.5 feet, and reoccurs three levels above and reaches a maximum at 12 feet. Always its amounts are insignificant.

South of the present boundary of the Lake Forest region *Tsuga* is usually weakly represented in pollen profiles, as it is in the present forests. Potzger ('46) draws the line in Michigan between the towns of Farwell and Shelby. In some southeastern Michigan profiles (Sears, '42a), *Tsuga* appears early with *Quercus*; in others, as at Sodon, its appearance is late, as it is in the neighborhood of the prairie peninsula. Potter ('47) compares *Tsuga* with the cool-moist deciduous climax species of *Acer* and *Fagus*, and Sears ('42b) considers it to have migrated westward in the Atlantic Period III, although

it may also have had a refugium in the Wisconsin driftless area.

Table II and figures 1 and 2 show that all the genera, while revealing evident trends, are subject to more or less strong oscillations in percentage representation in successive spectra or groups of spectra. Until there are good horizon markers for the changes from one period to another, it does not seem very profitable to attempt much interpretation of oscillations or minor trends. Between the well marked Periods I and II this was feasible. On the other hand, it does not seem possible to indicate just where in the Sodon Lake sediments one finds the transition from the Atlantic Period III to the sub-boreal Period IV. It is somewhere between the 19- and the 13-ft. levels. In fact, the transition from the boreal (which includes in the late boreal the rise of mesophytes) to the Atlantic period cannot be sharply marked on a basis of our data. Is it between 20 and 22, or as late as 19 feet? The answer to such questions depends upon the weight given to different genera in the interpretation of mesophytism. *Acer* indicates an earlier Atlantic period and *Tilia* a later one than do *Fagus* and *Tsuga*.

Period IV

The sub-boreal period is considered the second and strongest retrogression. It is a warm-dry period and, where well-marked, is called the xerothermic period by American students. Profiles of the Central Deciduous type in the North Central States generally show a long period of *Quercus* dominance with which is associated a relatively strong representation of *Carya* and a depression of the percentages of such mesophytes as *Fagus*, *Tsuga*, etc. Often during this period, which is long in terms of sedimentary column whether or not it is long in time, in about its upper third, there is a briefer period where still more dry conditions are indicated. This is marked by increase of *Carya* and in some places of grass, with a further depression of *Tsuga*, *Fagus*, etc.

This shorter interval in the longer period of *Quercus* dominance may be indicated in the Sodon Lake profile between 6-8 feet. There is a rise of *Pinus*, small rises of *Carya*, and depressions of *Acer* and *Fagus*. Once again, however, all we can point out is the general long dominance of *Quercus* as representative of the sub-boreal, with a possible accent of the trend at 6-8 feet. The latter is not convincing, however, but is more of a "looking for significance." Potter ('47), for example, found the Period IV maximum at about 80 per cent of the distance from the *Pinus* peak (II) to the surface, for several averaged Ohio profiles that were complete, which is near the 6-8 feet level in our profile. Smith ('40) felt that many of the minor oscillations, since they were matched from profile to profile, were very important in stratigraphic correlations. We do not feel that we can profitably employ those indicated in the present profile, but it is interesting to note the parallel behavior of certain genera, and the converse behavior of others. For example, during the period of general *Quercus* dominance, we find *Betula*, *Acer*, *Tilia*, and *Fagus* percentages rising together at 15, 13.5, and 5-5.5 feet, etc. On the other hand, *Tilia* and *Fagus* often complement one another, *Tilia* being low and *Fagus* high at 17 and 10 feet, and the converse at 16, 14, and 8 feet.

The absence of a well-marked, comparatively short xerothermic period in this profile is not destructive to the hypothesis that one occurred. Although Sodon Lake is not far north of the so-called prairie peninsula, which extended eastward into Ohio, it need not reflect strongly any changes. Potzger ('47) states that no Indiana profile in the region of the prairie peninsula indicates a replacement of forest by grassland. Since we are not distinguishing the species of *Quercus*, or of *Acer* and *Betula* for that matter, strong ecological changes could go undetected in the spectra. Furthermore, although Sodon Lake is located in a region where the climatic climax is now beech-maple, the

climax actually has been attained only on a comparatively small percentage of the land. Much more land, before lumbering, was *Quercus* dominated, mostly by late subclimax or successional stands, but some probably by preclimax relics. The xerothermic period is more strongly marked northward in the Lake Forest region and eastward in the more oceanic region of the Atlantic states than it is in southern Michigan. Sears ('42b) points out that the only appearance of *Carya* in the sediments northward of its present area is in connection with the occurrence of the *Quercus* maximum. This matches with the decrease of *Fagus* and *Tsuga* often found further southward.

The genus *Quercus*, being a large one, contains ecologically diverse species, the distinction of which would be a great boon were it possible in pollen studies. Taken as a whole, however, the species of *Quercus* are always used as an indication of drying conditions when their numbers increase. In our area the most mesophytic species, the northern red oak (*Quercus rubra*, syn. *Q. borealis* var. *maxima*), is normally succeeded by *Fagus*, and it extends farther toward the grassland formation than does *Fagus* (Sears, '42b). In the southern Appalachians the upper altitudinal limits for this oak are lower than those of *Fagus*, which forms subalpine stands at 5,000 feet or more and commonly is intermingled with *Picea*. The general climatic indications of *Quercus*, then are clear enough even though edaphic species requiring high water table and mesophytic species cannot be separated from the predominantly more xerophytic ones in the pollen spectra.

Period V

This is the recent period which seems to be cooler and more moist than IV. It corresponds to the sub-Atlantic of European chronology and is marked by an increase of *Picea* northward and of *Pinus* southward in the coniferous region from Minnesota to the Atlantic. North Cen-

tral profiles often do not reflect this change which, as yet, is apparently slight (Sears, '35). The Sodon profile is not convincing as to the existence of Period V, although slight rises are registered at the surface or at 6 inches by *Betula*, *Acer*, *Fagus* and *Tsuga*.

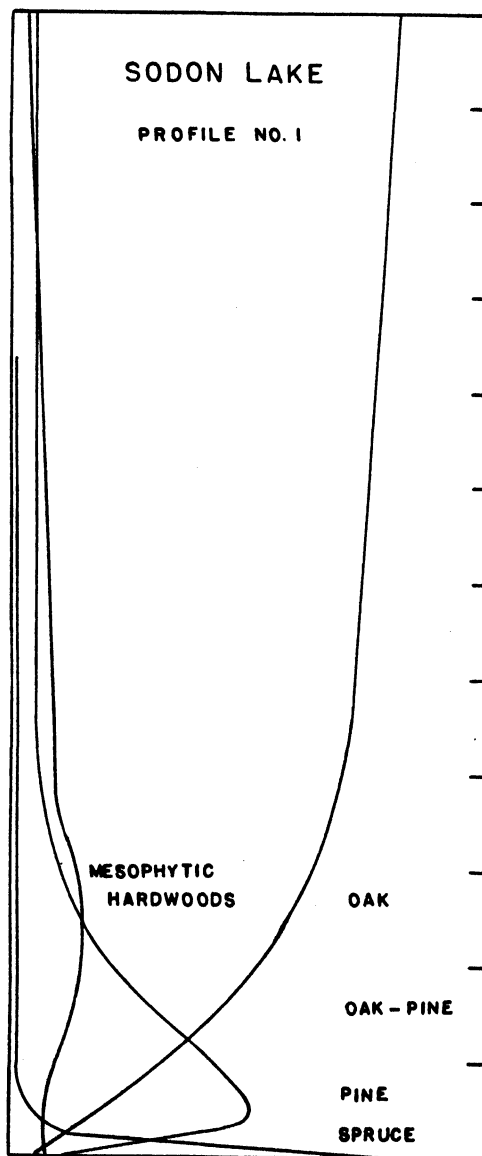


FIG. 3. Schematic representation of important ecological groups as represented by pollen grains. The curves have been smoothed by repeated running averages.

CONCLUSIONS

The general features of the profile are illustrated in the greatly simplified curves of figure 3, which should be compared with the detailed curves of figures 1 and 2. These curves have been smoothed by repeated series of running averages, taken by threes, and finally by inspection of the resulting positions.

The profile indicates that the lowest sediments, the blue clay layer at 24 feet, were deposited during the pre-boreal period or at the time of the final ice-sheet maximum for the area, when *Picea* forests prevailed. There is no doubt but that Profile I is truncated at the bottom, but it is also likely that the *Picea* period was short—in terms of height of sedimentary column—for the Sodon Lake profile is typical of many Central Deciduous profiles. Period II, of Sears' system, which is marked by *Pinus* dominance on the spectra, is also plainly evident at Sodon Lake. Concomitant with the decline in importance of *Pinus* is an equivalent rise of *Quercus*. The profile from 20 to 22 feet may well be described as a *Quercus-Pinus* period during which the mesophytic genera increase in importance. At no place in the profile are the deciduous, mesophytic genera of very great importance, but collectively they are of relative importance between about 15 and 21 feet. The outstanding character of the upper two-thirds of the profile is the continuing dominance of *Quercus*.

No short-time, pronounced xerothermic Period (IV) is evident in the Sodon Lake profile, and the final period reversion (V), so well-marked northward, is scarcely apparent at Sodon. The somewhat moister Atlantic Period III exists in the profile, but its limits cannot be set satisfactorily.

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NOTES AND COMMENT

TEMPORARY CHANGES OF CERTAIN LIMNOLOGICAL CONDITIONS IN WESTERN LAKE ERIE PRODUCED BY A WINDSTORM

INTRODUCTION

The effect of wind on movement of water which in turn influences the horizontal distribution of organisms and inorganic suspended matter is known to be important. The most commonly observed after-effects of wind action are temporary drifts of phytoplankton (Welch, '35) and irregularities in the vertical and horizontal distribution of zooplankton (Birge, '98). There are reasons to believe that wind action is also responsible in part for less conspicuous limnological changes in water masses. These changes occur and are likely to be unnoticed unless observations on the body of water in question have been continued for prolonged periods, which afford the investigator enough time to become thoroughly acquainted with the trends of its limnological characteristics.

Such characteristics of western Lake Erie have been studied the year round since 1938 (Chandler, '40, '42, '44, and Chandler and Weeks, '45). Phytoplankton, zooplankton, and various physical-chemical data compiled from these and more recent, unpublished studies show that western Lake Erie is composed of two distinct masses of water—one in the northern and one in the southern part of the lake. The movement and characteristics of the northern mass of water are influenced chiefly by the discharge of the Detroit River, whereas the southern body is influenced primarily by the discharge of the Maumee River. The over-all flow of the lake is slowly northeastward at a rate of 2 or 3 feet per minute (about one-fourth mile per day). The morphometry of the lake is such that winds from the northeast or southwest have perceptible influences on the water movements

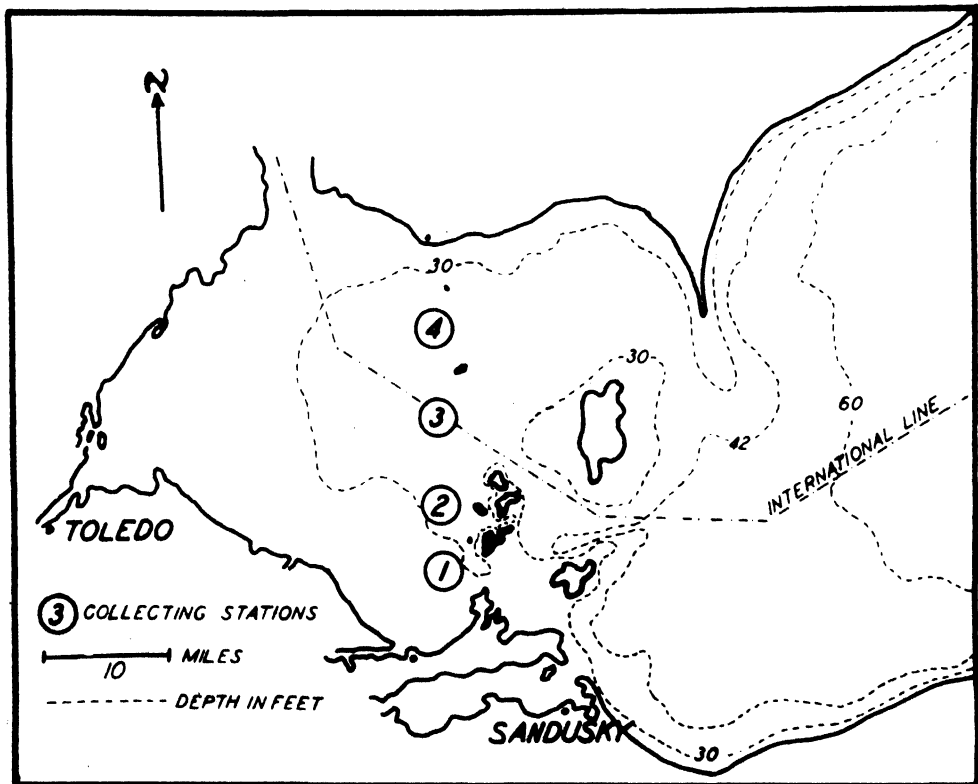


FIG. 1. Western Lake Erie showing relative positions of the 4 collecting stations. The international boundary line west of the island archipelago is approximately 1 mile north of the transition zone of the two limnologically distinct masses of water.

and these are reflected in changes of certain limnological characteristics in the two bodies of water. Since the transition zone of these two limnologically distinct areas is somewhere between stations 2 and 3, reference will not be made to variations at these stations; especial reference will, however, be made to characteristic trends and variations in conditions at stations 1 and 4 (figure 1).

The purpose of this report is to present the changes in certain limnological conditions of the two water masses immediately following a northeast windstorm in which the average velocity was 24.3 m.p.h. for more than 100 hours. Limnological changes that were recorded are: (1) wind direction and velocity; (2) lake level; (3) horizontal variations in turbidity, seston and temperature; and (4) horizontal variations in abundance of Cyclops and Diaptomus.

The writer is indebted to Dr. D. C. Chandler and W. J. Jahoda for data on seston and turbidity and for helpful suggestions during the preparation of this paper. For constructive criticisms regarding presentation thanks are due, also, to other members of the staff.

METHODS AND EQUIPMENT

Wind velocity and direction were recorded by a Friez electrical anemometer. Variations in lake level were taken from a lake level recorder which is furnished by the U. S. Lake Survey and is maintained and serviced at the Stone Laboratory.

Water samples for purposes of determining turbidities were taken at zero m., 5 m., and 9 m. with a modified Kemmerer water bottle, or they were taken only at zero m. with a clean dipper. A Coleman Model 11 spectrophotometer, which had been calibrated previously with a Jackson turbidimeter, was used to make the transmission measurements. All such measurements were made at 720 $m\mu$ (7200 Å). Calibration curves were prepared from the transmission values by using suspensions of diatomaceous earth in distilled water. The turbidity values for the diatomaceous suspension were determined with the Jackson Turbidimeter.

Seston, the total suspended matter, was determined for a liter sample taken at zero m., 5 m., and 9 m. Determinations were made according to a standard procedure which is discussed in detail elsewhere (Chandler, '42).

A Negretti and Zambra reversing thermometer was used to make all temperature determinations. Temperatures were taken at zero m., 5 m., and 9 m.

Zooplankton samples were taken with the 10 liter plankton trap at 1 m. intervals from surface to bottom. All adult and immature Cyclops and Diaptomus were enumerated; the adults were identified to species. The total number collected from all depths at any given station was recorded.

OBSERVATIONS

Wind. Wind action produces striking effects on the limnological conditions of the water in western Lake Erie. At 1800, April 18, 1947, the wind changed directions from the southwest to the northeast where it remained until April 23. The initial velocity was about 10 m.p.h., and by 0600, April 19, it was 26 m.p.h. From then until midnight, April 22, the average velocity was 24.3 m.p.h., with a maximum of 42 m.p.h. Since the axis of the lake is northeast-southwest, this wind produced noteworthy water movements. The result was a seiche wherein the southwest end of the lake had greatly increased water levels and water movements. Table I gives the duration, the average daily wind velocities, and the lake levels before and after the storm. The highest average daily velocity and the highest average daily water level occurred on April 21, after which the magnitude of the wind and the elevation of the lake level declined.

TABLE I. *Average wind velocities and directions and lake levels recorded during the windstorm.* Wind velocity is expressed in miles per hour and elevation of water level in feet referred to the mean tide at New York

| Date | Wind velocity (m.p.h.) and direction | Lake level (ft.) |
|----------------|--|---------------------|
| April 19, 1947 | 23.6 NE | 572.2 |
| April 20, 1947 | 28.8 NE | 573.9 |
| April 21, 1947 | 31.9 NE | 574.1 |
| April 22, 1947 | 14.5 NE | 573.4 |

Turbidity. The most obvious change in the limnological conditions in western Lake Erie following the action of a strong wind is evident in the turbidity of the water. The southern part of the lake is shallow, less than 10 m.; therefore strong winds completely circulate the water and increase its turbidity by resuspending materials. Another source of turbidity is discharge from the rivers in the southwestern part of the lake.

On April 23, 1947, two days following the peak of the windstorm, the wind and water calmed and it was possible to collect at the 4 stations shown in figure 1. This collection trip was one of a series that was started on April 4. On each occasion water samples were taken for purposes of determining the turbidity, seston, and standing crop of Cyclops and Diaptomus. The turbidities determined from water samples taken at the 4 stations before and after the storm are compared in table II where each number represents an average of the turbidities determined for zero m., 5 m., and 9 m. Since the water was uniformly turbid, the samples were averaged.

TABLE II. *Comparison of turbidities from samples taken before and after the windstorm. Data collected immediately following the windstorm are underscored.*

| Date | Turbidity (p.p.m.) | | | |
|----------------|--------------------|-------------|-------------|-------------|
| | 1 | 2 | 3 | 4 |
| April 4, 1947 | 76.0 | 75.5 | 32.8 | 28.1 |
| April 14, 1947 | 34.3 | 34.3 | 23.4 | 24.2 |
| April 23, 1947 | <u>15.6</u> | <u>11.7</u> | <u>26.5</u> | <u>55.4</u> |
| May 9, 1947 | 112.5 | 56.2 | 56.2 | 42.1 |
| Station | 1 | 2 | 3 | 4 |

It may be seen that on April 4 the turbidity decreased from 76.0 p.p.m. at station 1 to 28.1 p.p.m. at station 4. Past experience has shown that this is the usual trend, although the actual values may fluctuate greatly from time to time. Further inspection of the table shows that similar trends were exhibited in the April 14 and May 9 samples. But, on the other hand, the turbidities of the April 23 samples indicate a reversal of the usual tendency. The water at station 4 was more turbid.

To study further the effect of the wind on the turbid conditions, two surveys were made of the entire western end of the lake. Surface samples were taken and their turbidities ascertained. It was not necessary to sample at different depths, since strong winds insure com-

plete mixing and, as a result, nearly uniform vertical turbid conditions. Figure 2 gives, in general, the distribution of the turbid water sampled in the above surveys. A large mass of relatively clear water, 12.0 to 30.0 p.p.m., was found south and west of the island region and a large expanse of very turbid water, 100.0 to 217.0 p.p.m., extended from the mouth of the Maumee River in the southwest corner across the lake towards the northeast. From these results it was deduced that the northeast wind had forced a mass of water towards and along the south shore. This mass of water deflected the turbid discharge of the Maumee River causing it to traverse the lake and then follow eastward along the north shore. This accounts for the water being more turbid at station 4 than at 1 immediately following the windstorm.

Seston. For purposes of comparing the total standing crop at each of the 4 stations before and after the windstorm, total seston, total suspended matter—determinations were made from water samples taken at zero m., 5 m., and 9 m. The values ascertained from samples at these depths were averaged for stations before and after the storm and recorded in table III. The amount of suspended matter in the water usually is greater at station 1 than at station 4. Such trends are shown in the April 4, 14 and May 9, 19 collections. This usual tendency was found to be reversed in the April 23 samples. This reversal was expected, after it was



FIG. 2. An outline map of western Lake Erie showing the distribution of turbid water in p.p.m. following the windstorm. The magnitude and direction of the wind are indicated.

TABLE III. *Horizontal variations in total seston before and after the windstorm.* Data collected immediately following the windstorm are underscored

| Date | Seston (mg./l.) | | | |
|----------------|-----------------|------|------|------|
| April 4, 1947 | 44.0 | 37.0 | 21.0 | 17.0 |
| April 14, 1947 | 31.0 | 19.0 | 14.0 | 16.0 |
| April 23, 1947 | 13.0 | 11.0 | 15.0 | 33.0 |
| May 9, 1947 | 56.0 | 55.0 | 25.0 | 20.0 |
| May 19, 1947 | 11.0 | 11.0 | 11.0 | 8.0 |
| Station | 1 | 2 | 3 | 4 |

shown that the turbid discharge of the Maumee River had been deflected away from station 1 towards station 4.

Temperature. Temperature is another limnological condition in which the two bodies of water differ. The water in the southern part of the lake, due to its tributaries and its shallowness, warms more rapidly in the spring than the water in the northern part. As a result the temperature of the water decreases as one progresses northward from station 1. Temperatures obtained at zero m., 5 m. and 9 m. at each station were averaged and recorded in table IV. The readings of April 4, 14 and of May 9, 19 demonstrate the usual spring trends in temperature. The change in this tendency in the April 23 and May 9 readings indicates, further, that the windstorm by producing movements of water had altered the temperature characteristics of the two bodies of water.

Cyclops and Diaptomus. In the early spring Cyclops and Diaptomus comprise more than 99 per cent of the entomostracan population of all stations. For example, at station 1 on April 4, Diaptomus represented 47.7 per cent and Cyclops 52.0 per cent of the total entomostracan population (table V). Daphnids comprised the remaining 0.3 per cent. The variations in the daphnid distribution were not included, since Cyclops and Diaptomus were predominate. Previous to and following the storm, 10 liter water

TABLE IV. *Horizontal variations in temperature before and after the windstorm.* Data collected immediately following the windstorm are underscored

| Date | Temperature (° C.) | | | |
|----------------|--------------------|------|------|------|
| April 4, 1947 | 1.3 | 1.3 | 1.1 | 0.8 |
| April 14, 1947 | 6.4 | 4.8 | 3.4 | 3.4 |
| April 23, 1947 | 4.9 | 4.6 | 4.7 | 4.7 |
| May 9, 1947 | 8.3 | 8.4 | 8.0 | 8.0 |
| May 19, 1947 | 12.4 | 11.6 | 11.7 | 10.5 |
| Station | 1 | 2 | 3 | 4 |

samples were taken at 1 m. intervals at each station and all individuals of Cyclops and Diaptomus were enumerated and expressed in per cent of the total entomostracan population. Inspection of the table shows that a smaller percentage of diaptomids occurred at station 1 than at station 4. Collections of April 4, 14 and May 9, 19 indicate the usual tendency of distribution. Immediately following the windstorm, April 23, this trend was reversed, a larger percentage occurred at station 1 than at 4. Typical trends in the Cyclops distribution are shown to bear reciprocal relationship to those of Diaptomus. It may be seen in the April 4, 14 and May 9, 19 collections that a greater percentage of Cyclops occurred at station 1 than at 4. However, after the windstorm, April 23, the usual trend was reversed—a greater percentage of Cyclops was at station 4.

TABLE V. *Horizontal variations in abundance of Cyclops and Diaptomus expressed in per cent of the total entomostracan population before and after the windstorm.* Data collected immediately following the windstorm are underscored

| Date | Diaptomus (%) | | | |
|----------------|---------------|------|------|------|
| April 4, 1947 | 47.7 | 43.1 | 69.7 | 80.9 |
| April 14, 1947 | 25.2 | 31.0 | 86.6 | 73.6 |
| April 23, 1947 | 69.7 | 76.4 | 42.2 | 43.3 |
| May 9, 1947 | 36.9 | 41.0 | 36.1 | 49.8 |
| May 19, 1947 | 20.9 | 17.7 | 28.9 | 23.8 |
| Cyclops (%) | | | | |
| April 4, 1947 | 52.0 | 56.9 | 30.3 | 18.5 |
| April 14, 1947 | 74.8 | 68.9 | 13.4 | 26.4 |
| April 23, 1947 | 29.7 | 23.1 | 57.3 | 56.2 |
| May 9, 1947 | 63.1 | 57.6 | 61.5 | 47.7 |
| May 19, 1947 | 77.6 | 81.8 | 71.1 | 75.4 |
| Station | 1 | 2 | 3 | 4 |

CONCLUSIONS

From these data it seems apparent that the windstorm, by producing movements of water, reversed the usual tendency in the horizontal variations in (1) seston, turbidity, and temperature; and (2) abundance of Cyclops and Diaptomus. Further, it is reasonable to believe that winds of lesser magnitudes probably produce similar but less striking variations in the horizontal distribution of zooplankton, phytoplankton, and suspended inorganic matter in natural waters.

SUMMARY

1. The after-effects of a northeast, April windstorm on certain conditions in two limno-

logically distinct bodies of water in western Lake Erie are presented.

2. Limnological changes that were recorded are: (1) wind direction and velocity; (2) lake level; (3) horizontal variations in turbidity, seston, and temperature; and (4) horizontal variations in abundance of Cyclops and Diaptomus.

3. Turbidity determinations indicated that the windstorm forced a large mass of water toward and subsequently along the south shore. This water mass deflected the turbid discharge of the Maumee River from its usual southern route northeastward across the lake and along the north shore.

4. The usual trends in turbidity, seston, and abundance of Cyclops and Diaptomus were reversed by the windstorm. The usual temperature changes were not reversed; however, they were varied considerably.

5. It is suggested that windstorms of lesser magnitude might produce similar but less striking variations, and that these changes are likely to be unnoticed unless the usual tendencies of the limnological conditions are determined first from the results of prolonged studies.

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TED F. ANDREWS

FRANZ THEODORE STONE LABORATORY,
THE OHIO STATE UNIVERSITY,
PUT-IN-BAY, OHIO

OBSERVATIONS ON THE EFFECT OF FLOOD ON ANIMALS

The summer of 1945 provided an opportunity to observe the effects of a short-duration flood on some of the bottomlands animals of the Patuxent Research Refuge, Laurel, Maryland.¹ Ability of animals to survive flood conditions is important, for large areas of flood plain in eastern coastal plain valleys are washed over periodically. The floods last a relatively short time and do only minor damage to vegetation. They are not comparable to the devastating floods described by Blair ('39) and Grinnell ('39) in Oklahoma and California. The floods described by these authors were so extensive and of such duration that herbaceous and shrubby vegetation was killed. Mammal populations were nearly eliminated and reinvasion of the area was exceedingly slow. The Illinois winter floods described by Yeager and Anderson ('44) were also severe and of long duration. Their observations include notes on the squirrels and raccoons that continued to occupy the flooded woodlands, as well as a more detailed study of the animals of several species that were concentrated on the levees.

¹The physiography, topography, and vegetation of the Refuge are described by Hotchkiss and Stewart ('47).

The flood discussed here resulted from heavy rainfall in the drainage system of the Patuxent River. Rain began the afternoon of July 14, 1945, and continued more or less steadily through July 19, producing the most severe flood in several years. The peak came in the afternoon of July 18. By July 25 the flood waters had receded, though most of the drainage channels were filled with running water.

The entire bottomlands area, one-quarter to one-half mile in width, was submerged to a depth of more than three feet. No land remained above water at any point. The natural drainage channels that lace the area could be distinguished as regions of swift current. When the flood waters subsided it was seen that the leaf cover of the forest floor had been swept away, leaving bare ground over much of the area. Heaps of leaves were piled with other debris against tree bases and bushes. Many of the familiar landmarks provided by logs and brush heaps were washed away or deposited in new places. Herbaceous vegetation was flattened and much of it killed. Shrubby growth near channels was temporarily bent over. Less severe floods occur one or more times each year, but in these the water does not cover the

higher portions of the bottomlands. Some land remains above water even at flood peak and when the flood subsides there is little sign of its presence except for washing near the channels.

Observations during flood. A thirty-acre wooded area that had been studied through the season provided favorable conditions for observations of flood effects. Several trips were made into the bottomlands near flood peak. At this time nearly every bit of emergent brush and all tree bases supported masses of insects, spiders, and other invertebrates of many kinds. *Spirobolus marginatus*, other millipedes, and ground beetles were especially numerous and conspicuous, actually weighting down the branches of many shrubs. Floating rafts of wood and debris were also refuge points for many animals.

Near the peak of the flood, the afternoon of July 18, Robert Stewart, Robert Mitchell, and James Cope worked their way across the study area and back, a 1640 yard trip that occupied the better part of the afternoon. They avoided getting into the main river channel by following painted blaze marks that pointed an east-west route across the area. They observed and recorded the following vertebrate animals:

Plethodon c. cinereus: numerous on vegetation; 15 swimming.

Ambystoma opacum: 2 swimming.

Bufo terrestris americanus: several.

Bufo woodhousei fowleri: 1 or more.

Carphophis a. amoena: 2 swimming.

Elaphe o. obsoleta: 1 swimming.

Terrapene c. carolina: 18; on debris, swimming, or floating.

Pitymys p. pinetorum: 14 floating on debris, mostly wet.

No *Peromyscus leucopus* were seen, although they were the most numerous small mammals in the habitat.

Wood mice. As part of a DDT study, *Peromyscus leucopus* had been trapped in the bottomlands area in two different periods preceding the flood. The area was trapped again immediately following the flood to determine possible effects on this semi-arboreal species.

There were two study plots. One was a two-acre river island connected with the mainland by several logs across the river and by overhanging trees. Twenty-five live traps were distributed fairly uniformly over the island in favorable sites. The other trapping unit, on the mainland, consisted of twenty-five traps spaced 165 feet apart in a grid arrangement over a ten-acre area. Traps were operated for five days in each of three periods. The first two periods, May 2-7 and June 14-19, preceded the flood and the third period, July 23-28, came immediately after the flood.

The numbers of mice captured in the different trapping periods were compared to see if the flood had caused a noticeable reduction. It was found that there was no significant difference in the number collected in the period just before the flood and the period following it (table I).

TABLE I. *Wood mice trapped before and after the flood*

| Plot A (river island) | Before flood | | After flood |
|--|--------------|------------|-------------|
| | May 2-7 | June 14-19 | July 23-28 |
| Number of individuals captured | 40(7)* | 30(2) | 38(2) |
| Number released (number captured minus number died in traps) | 24(6) | 30(2) | 38(2) |
| Repeats from preceding period | — | 10 | 14 |
| Plot B (mainland) | | | |
| | | | |
| | | | |
| | | | |
| Number of individuals captured | 54(17) | 25 | 22 |
| Number released (number captured minus number died in traps) | 39(12) | 25 | 22 |
| Repeats from preceding period | — | 10 | 13 |

* Numbers in parenthesis represent juveniles included in the group. All others were adult or subadult animals. The decrease in numbers between the first and second trapping periods, both preceding the flood, cannot be fully explained. It was perhaps due in part to the larger number of juveniles in the first period and in part to the heavy trap mortality that period.

Trapping results were also compared on the basis of proportional returns between periods. The proportion of repeats before and after the flood were not significantly different from the proportion of repeats between the two periods before the flood.

Mice retaken in successive periods were found to have traveled about as far between each of the periods as they did within a single period. It was evident that the constancy of the mice to their home ranges was not affected by the flood.

The effect of the flood on the wood mouse population as a whole was negligible, though it is probable that certain individuals were lost or left the area. The success of the members of this species is probably largely attributable to their arboreal tendencies, but may also have been aided by their swimming ability (Teeters, '45).

Box turtles. In the transect of the study area that was made near flood peak, 18 box turtles

were seen on debris or in the water. Additional observations were made in another similarly flooded bottomlands area where a detailed study of these animals was in progress.

The home ranges of many of the turtles had been determined by numerous collections that year and the preceding year. Most of the turtles in the population had been marked. When the flood had subsided enough to show some emergent land the area was searched for box turtles.

On July 19 and 20, 25 box turtles were collected in the study area. Eighteen of them had been collected often enough previously that their ranges were fairly well known. Of these 18, one turtle apparently had been carried by the flood waters, for she was found 670 feet from the nearest portion of her normal range. Eleven days later she was found within her normal range, and was collected there eight more times in the season. Two others may or may not have been moved by the flood; they were found 170 feet from the nearest known parts of their home ranges. The remaining 15 evidently were not displaced, for their flood records were within their normal ranges.

Seven of the 25 turtles found during the flood had been collected fewer times, so their status in the population was less clear, and their flood records were correspondingly less subject to interpretation. With two exceptions, however, they were collected during the flood at localities less than 150 feet from their other collection points. Thus these box turtles showed a remarkable ability to remain in their home ranges, even under the adverse conditions of a severe flood.

Collections before and after the flood were compared to see if resident turtles had been removed by the flood or new turtles brought in. No differences were found between the proportion of marked and unmarked turtles collected in 10-day periods before and after flood. It was also found that very nearly all of the individuals collected in the study area before the flood were present after the flood. It is particularly interesting that such weak swimmers

as box turtles were able to maintain home ranges and virtually unchanged populations despite the flood.

Acknowledgments. Particular acknowledgments are due to Clyde Vance for assistance in the mammal trapping and turtle collecting, and to Robert Stewart, Robert Mitchell, and James Cope for their notes on animals seen at the flood peak.

Summary. The flood plain of the Patuxent River is washed over periodically, and occasionally the entire bottomland is submerged to a depth of several feet. The effects of an unusually severe flood on the populations and home ranges of wood mice (*Peromyscus leucopus*) and box turtles (*Terrapene carolina*) were studied by means of collecting the animals before, during, and after the flood. The flood had little or no effect on the size of the populations, and individuals showed remarkable ability to remain within their home ranges despite the flood.

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LUCILLE F. STICKEL

PATUXENT RESEARCH REFUGE,
LAUREL, MARYLAND

FOG AND ATMOSPHERIC CARBON DIOXIDE AS RELATED TO APPARENT PHOTOSYNTHETIC RATE OF SOME BROADLEAF EVERGREENS

During an investigation of the rate of apparent photosynthesis of *Camellia japonica* L. and *Ligustrum lucidum* Thunb., carried on during the winter months, it was observed that the presence of fog was always accompanied by a substantial increase in the rate of apparent photosynthesis. On foggy mornings, the rate of apparent photosynthesis was usually higher than

on clear mornings having similar temperatures and light intensities.

The plants used in this experiment were growing in 12" pots located on the roof of a three-story building. Rate of apparent photosynthesis was determined by measuring the difference in concentration of carbon dioxide present in the air before and after it was passed over the leaves

TABLE I. *The rate of apparent photosynthesis of Camellia japonica on foggy mornings as compared to clear mornings with similar light and temperature*

| Mg. CO ₂ /liter before passing over leaf | Mg. CO ₂ /liter after passing over leaf | Rate of apparent photo-synthesis, mg. CO ₂ /100 cm. ² /hr. | Light, g. cal/cm. ² /min. | Temperature °C. |
|---|--|--|--------------------------------------|-----------------|
| Foggy | | | | |
| .67 | .63 | 1.56 | .133 | 4 |
| .70 | .54 | 7.68 | .665 | 12 |
| .67 | .60 | 3.36 | .798 | 14 |
| .67 | .59 | 3.60 | .732 | 5 |
| .68 | .58 | 5.04 | .798 | 8 |
| .67 | .64 | 1.68 | .266 | 4 |
| .67 | .60 | 3.36 | .931 | 8 |
| .67 | .60 | 3.36 | .665 | 7 |
| .72 | .65 | 4.32 | .798 | 10 |
| .69 | .63 | 3.00 | .638 | 11 |
| Clear | | | | |
| .56 | .55 | .24 | .199 | 4 |
| .56 | .54 | .64 | 1.064 | 2 |
| .54 | .52 | .84 | 1.064 | 6 |
| .54+ | .54 | .12 | .199 | 3 |
| .53 | .51 | .84 | .599 | 7 |
| .54 | .50 | 2.28 | .931 | 10 |
| .54 | .52 | 1.20 | 1.197 | 8 |
| .53 | .51 | 1.20 | .399 | 5 |
| .54 | .51 | 1.96 | .798 | 14 |
| .54 | .52 | 1.08 | .665 | 12 |

of the plants. The carbon dioxide content of the air was measured by passing the air streams through absorption towers and determining the

change in conductivity of the absorbing solutions. Light intensity was measured with a spherical thermocouple inclosed in an evacuated glass bulb and attached to a micromax recorder. Temperature was determined by a Friez Hygrothermograph located in a standard weather bureau instrument shelter which was adjacent to the plants. Leaf temperatures were determined by a copper-constantan thermocouple, one junction of which was braided through the leaf, the other maintained near the leaf but completely shaded. There was no significant deviation between the leaf and air temperature during the course of the experiment.

Measurements were obtained on ten days when there was perceptible to heavy fog, at least for a few hours in the mornings and on ten non-foggy days. On every foggy morning the carbon dioxide content of the air was 20 to 25 per cent above normal. The data for ten foggy mornings and for ten non-foggy mornings having similar light intensities and temperatures are summarized in table I.

Fog has been considered to favor plant growth through its effect on moisture content. The moisture content of the leaves of the plants used in this experiment was not determined but it appears unlikely that it was low enough to be a limiting factor on photosynthesis even on the fog-free days. A more probable explanation for the increased photosynthesis on foggy mornings is that it results from the higher carbon dioxide concentration of the air on such mornings.

This observation may have an application to those regions where maximum plant growth is associated with prevalence of fog.

C. C. WILSON

DEPARTMENT OF BOTANY,
UNIVERSITY OF GEORGIA,
ATHENS, GEORGIA

PLANT SUCCESSION ON FALLEN LOGS IN A VIRGIN SPRUCE-FIR FOREST¹

The author wishes to express his appreciation to Dr. A. O. Weese and Dr. H. G. Barclay for their suggestions regarding the problem.

During the summer of 1946 a study was made of the plant succession on fallen logs in the Gothic Natural Area of the Gunnison National Forest about ten miles north of the town of Crested Butte, Gunnison County, Colorado. The Gothic Natural Area is a region of virgin forest of the Sub-Alpine Spruce-Fir climax which has been set aside by the Forest Service for biological research under the direction of the Rocky

Mountain Biological Laboratory. The area extends for about one mile parallel to the East River and from an elevation of 9,800 feet to above timberline, a distance of about two miles.

The present study was limited to an area of about five acres on both sides of Quigley Creek at an altitude between 9,800 and 9,900 feet. The region contains three distinct types of conditions: mesic, bog, and xeric. The mesic areas occupy the northern portion of the region studied and extend to within two hundred feet of Quigley Creek. The xeric parts occupy the rocky, east-facing slope located south of Quigley Creek and a knoll rising to 9,900 feet near the entrance of the research area. The bog parts of the region are located along the northern side of Quigley Creek. In several places here and also on

¹ Contribution from the Rocky Mountain Biological Laboratory, Crested Butte, Colorado and the Biological Laboratories, Howard College, Birmingham, Alabama.

the steep slope which borders the creek on the south there are vertical bogs caused by seepage.

Each of the different types of habitat was considered separately in the collection of data and each indicates a different modification of the general pattern of succession on the fallen logs. One hundred fifty-three logs of various lengths were studied in the three habitats. No attempt was made to distinguish between logs of the

two climax trees (*Picea Engelmannii* and *Abies lasiocarpa*) throughout the work since the difference between the logs of the two species is very difficult to distinguish in the field once the bark is gone. In each habitat several stations were selected as being typical (5 mesic, 3 bog, and 2 xeric) and observations on the vegetation and conditions of the logs were recorded. In order to verify the general data, a quadrat ten

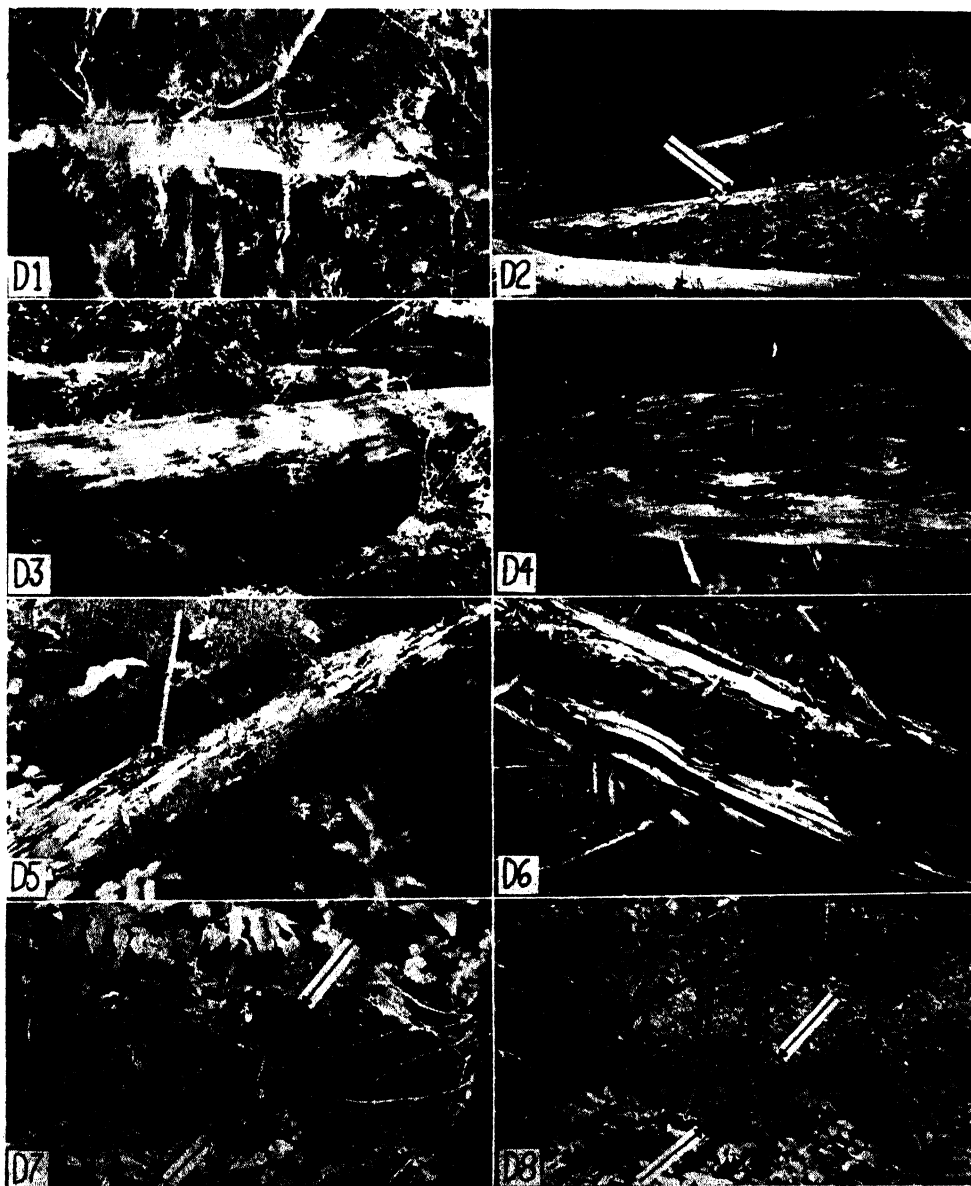


FIG. 1. Fallen logs of typical decay classes. Decay class is indicated on each photograph. Where necessary, arrows are used to distinguish the log being considered.

meters square was laid off in each habitat. The logs in each quadrat were charted and actual vegetation counts were made upon them. In both the logs of the quadrats and those of the various stations the fungal, lichen, hepatic, and moss vegetations were recorded in per cent of coverage for each log. Combined counts according to the size of the plants were made of the seedlings of the climax trees on each log of both the quadrats and the stations. Vegetation counts were made for flowering plants only on the logs of the quadrats; those of the logs of each station were recorded merely as to degree of frequency.

For each log, information on the diameter, length, position, and condition of decay was obtained. Decay stages suggested by Ingles ('33) were inadequate for the present study so the following decay classes, designated as D1, D2, etc., were organized with the characteristics indicated. Figure 1 shows photographs of logs of each decay class.

D1—Freshly fallen trees with bark intact and needles (either green or dead) remaining on the branches which themselves are either intact or evidently broken from the trees in question.

D2—Fallen trees with bark intact but appearing dead, with or without evidence of bark breaking up. No large branches present.

D3—Fallen trees without bark but still solid or with bark broken up but evident in patches.

D4—Fallen trees definite in outline with the surface grain still evident but with decay initiated along the grain.

D5—Fallen trees definite in outline but with decay well advanced as indicated by the presence of loose fragments of wood.

D6—Fallen trees indefinite in outline with scattered fragments of wood evident.

D7—Fallen trees indefinite in outline, decay well advanced with few or no wood fragments present, or if present they may be easily crumbled.

D8—Fallen trees with decay practically complete and soil formed. Outline difficult to determine.

While the diameter of a log may control the length of time necessary for it to reach decay class D8, a small diameter log of a given class represents the same stage as far as plant succession is concerned as a large diameter log of the same class. In order to obtain comparable statistics, essential tabulations involving species counts by decay class (except those pertaining specifically to the ten-meter quadrats) are calculated on the basis of a unit of 100 meters of log length.

Names of seed plants follow the usage of Coulter and Nelson ('37) while Grout's ('28-40) nomenclature is used for the mosses.

GENERAL PATTERN OF SUCCESSION

The general pattern of succession is similar in the three different habitats. No evidence of any noticeable migration onto logs was visible until the logs reached decay class D2. The logs of class D1 had no indication of vegetation except for strands of *Usnea*, but since this epiphytic lichen was found in considerable quantities on erect living trees its occurrence is merely noted here and its presence is to be considered of no importance to the succession. The initial plants to move onto logs, appearing first in class D2, are forms of *Cladonia* and the tiny leafy liverwort, *Lophozia*. Following the establishment of this lichen-liverwort stage is the moss phase with *Brachythecium* as the chief genus. The *Cladonia-Lophozia* stage and the moss stage co-exist through several decay classes but the lichens and liverworts appear earlier in greater quantity than the mosses and give way in importance to the moss flora in the later decay classes. By decay class D4 herbaceous species begin to appear upon the logs. Here the initial plants depend upon the individual succession as will be discussed in the later paragraphs. *Vaccinium*, representing a stage in succession in this sere as indicated by Stahelin ('43), may appear if that plant is present in the immediate environment.

The presence of trees of the climax forest cannot be used as a criterion for recognition of completion of the succession on fallen logs. The chance of a mature tree growing from every log studied is small. Rather the appearance in quantity of the herbaceous and shrubby forms of the undercover in mature flowering and fruiting condition is sufficient evidence of the completion of the succession.

Numerous collections of fungus fruiting bodies were taken from the logs studied but only a very few species were ever found on more than one log. The following genera were most common: *Polyporus* (chiefly *P. albobuteus* Ell. & Ev., and *P. abietinis* (Dicks.) Fr.), *Omphalia* (chiefly *O. campanella* Fr. and *O. Epichrysium* Fr.), *Philiota marginata* (Batsch.) Fr., *Poria*, *Dialia*, *Guepiniopsis alpinus* (Tracy and Earle), and a tiny orange-colored ascomycete unidentifiable from available sources.² Fungus fruiting bodies appear first in decay class D2 and remain with little variation in number recorded until class D7 when a slight decrease in number is evident. Typically only a very few fungus fruiting bodies were present on any one log. An analysis of the data collected indicates no species or group of species of fungi as being associated specifically with any single stage or phase of the succession. It is thus apparent that the presence of fungi, while important to

² Identification of fungi was made by Dr. L. K. Henry, Curator of the Herbarium, Carnegie Museum, Pittsburgh, Pennsylvania.

TABLE I. Total seedling count of *Picea Engelmannii* and *Abies lasiocarpa* by seedling height classes and by log decay class in the three habitats studied. (Values are numbers of seedlings per 100 meters of log length.)

| | D1 | D2 | D3 | D4 | D5 | D6 | D7 | D8 |
|--------------|----|------|-------|--------|--------|--------|--------|--------|
| Mesic | | | | | | | | |
| 0-5 cm. | | 7.42 | 35.29 | 187.10 | 445.90 | 486.92 | 689.80 | 85.42 |
| 5 cm.-15 cm. | | | | 12.90 | 71.04 | 228.20 | 269.39 | 85.42 |
| 15 cm.-3 dm. | | | | | 6.55 | 58.14 | 24.49 | 45.83 |
| 3 dm.-1 m. | | | | | | 1.45 | 6.12 | 12.50 |
| Over 1 m. | | | | | | | 2.04 | 43.75 |
| Total | | 7.42 | 35.29 | 200.00 | 523.49 | 774.71 | 991.84 | 272.92 |
| Bog | | | | | | | | |
| 0-5 cm. | | | | 54.49 | 166.67 | 163.89 | 62.50 | 19.35 |
| 5 cm.-15 cm. | | | | | 69.73 | 97.22 | 79.16 | 2.15 |
| 15 cm.-3 dm. | | | | | 5.10 | 33.33 | 62.50 | 6.45 |
| 3 dm.-1 m. | | | | | 1.70 | 5.56 | 12.50 | 32.25 |
| Over 1 m. | | | | | | | 29.17 | 62.36 |
| Total | | | | 54.49 | 243.20 | 300.00 | 245.83 | 122.56 |
| Xeric | | | | | | | | |
| 0-5 cm. | | | | | 3.88 | | 33.33 | 414.81 |
| 5 cm.-15 cm. | | | | | | 14.29 | 27.78 | 111.11 |
| 15 cm.-3 dm. | | | | | | | | 3.70 |
| 3 dm.-1 m. | | | | | | | 5.56 | |
| Over 1 m. | | | | | | | | |
| Total | | | | | 3.88 | 14.29 | 66.67 | 529.62 |

the decay of the logs, is not of value in the determination of successional stages.

The chance of survival of an individual seedling of either of the climax trees may be slight but reference to table I indicates that survival does occur. The maximum numbers of seedlings were observed on logs (in the bog and mesic habitats) of stages D5 and D6. On logs of later stages the numbers were much smaller but many of the seedlings were several years old. In the xeric habitat the numerous seedlings on logs of the D8 stage were still very young. The germination of the spruce and fir seedlings can occur on logs of all decay classes from D2.

MESIC SUCCESSION

Under mesic conditions the lichen-liverwort stage consists of various species of *Cladonia* and of *Lophozia porphyroleuca* (Nees) Schiffner and *Lophozia incisa* (Schrad.) Dumont.³ These forms appear first in decay class D2 and reach their peak about D5 and D6. Usually the *Cladonia* is present in the greater quantity. The

³ Identification of the liverworts was made by Dr. Margaret Fulford, University of Cincinnati, Cincinnati, Ohio.

moss stage is represented by species of *Brachythecium*, *Dicranum* (chiefly *D. scoparium*), *Drepanocladus*, *Pohlia cruda* and *Plagiothecium denticulatum*. The several species of *Brachythecium* are dominant with *Pohlia*, *Dicranum*, and *Plagiothecium* being relatively important. As is evident in figure 2A the mosses first appear in D2 but they are distinctly later in reaching a dominant condition and remain on fully decayed logs (D8). The herbaceous species first appear in class D4 but it is not until the next class that they are present in quantity. The herbaceous stage is dominated by *Mitella* (*M. pentandra* and *M. stauropetala*) and *Listera convallarioides* with *Epilobium saximontanum* and *Streptopus amplexifolius* being important. Following the herbaceous stage is the low shrub stage which appears first in D6. *Vaccinium oreophilum* is the chief shrubby species in the succession with the herbs, *Arnica cordifolia* and occasionally *Pedicularis racemosa* accompanying this shrub in some places. Other species found on fallen logs in the mesic condition in the order of their total frequencies in the succession are: *Polemonium pulcherrimum*, *Luzula parviflora*, *Mertensia ciliata*, *Lycopodium annotinum*, *Lo-*

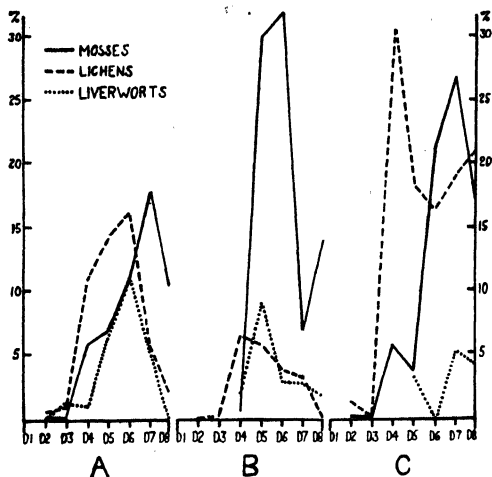


FIG. 2. Total per cent of coverage by decay class of lower plant forms. A. Mesic habitat. B. Bog habitat. C. Xeric habitat.

nica involucreta, *Ribes* sp., *Oxypolis Fendleri*, *Moneses uniflora*, *Pyrola minor*, *Washingtonia obtusa*, *Equisetum arvense*, *Senecio triangularis*, *Cardamine cordifolia*, *Aquilegia elegantula*, *Androsace septentrionalis*, *Parnassia* sp., *Taraxacum* sp., *Lysicella obtusata*.

BOG SUCCESSION

The lichen-liverwort stage in the bog areas has the same typical genera as in the mesic condition, *Cladonia* and *Lophozia*. *Cladonia* appeared first in D3 with *Lophozia* coming later

in D4. The moss stage, also, is similar to that of the mesic succession, appearing in quantity on slightly more decayed logs and remaining until the end of the succession (see fig. 2B). The chief moss is again *Brachythecium* which appears first in D4. *Mnium punctatum* and *M. punctatum elatum* are the only other important mosses, appearing first in D5. The herbaceous stage consists of two phases. The first has as dominants *Cardamine cordifolia* and *Equisetum arvense* with *Saxifraga arguta* and *Viola blanda* as important species. Later the importance of the saxifrage and the violet wanes, and their subdominance is replaced by *Mitella*. A distinct *Vaccinium* stage was not observed although a few individuals were found on logs in the area but only near the edge of the bog approaching mesic conditions. Other herbaceous and shrubby species found on logs in the bog in the order of their total frequency are: *Epilobium saximontanum*, *Streptopus amplexifolius*, *Oxypolis Fendleri*, *Senecio triangularis*, *Mertensia ciliata*, *Aconitum columbianum*, grasses (chiefly *Calamagrostis canadensis*), *Lysicella obtusata*, *Geranium Richardsonii*, rushes (chiefly *Luzula parviflora* and *L. spicata*), *Caltha rotundifolia*, *Listera convallarioides*, *Arnica cordifolia*, *Pyrola minor*, *Fragaria* sp., *Lonicera involucreta*, *Moneses uniflora*, *Trollius albiflorus*, *Ribes* sp., *Geum macrophyllum*, and *Taraxacum* sp.

XERIC SUCCESSION

Under the xeric conditions the decay of logs is a much slower process. The quantity of vegetation in this area as indicated by the species list is much smaller than for the other two habitats.

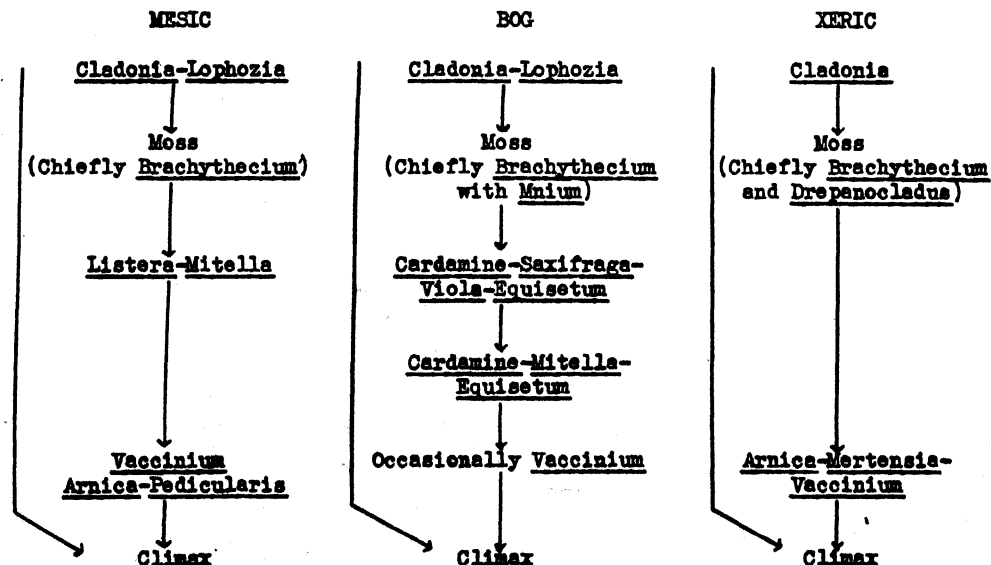


FIG. 3. Comparison of succession on fallen spruce and fir logs in the three habitats.

The lichen-liverwort stage becomes the lichen stage in the xeric succession. Only species of *Cladonia*, appearing first in D2, seem to be important here as the initial plants. The moss stage follows closely the lichen stage (see fig. 2C). *Brachythecium* is important but its dominance in the area studied is shared with species of *Drepanocladus* (chiefly *D. aduncus* and *D. uncinata*) which also first appear in D2. The first herbs appear in D5 but are not found in quantity until D7 is reached. The herbaceous stage seems to be combined with the *Vaccinium* stage with *Arnica*, *Mertensia*, and *Vaccinium* appearing about the same time and in about the same importance. Other species found in the order of their total frequency are: *Pyrola minor*, *Streptopus amplexifolius*, *Aquilegia elegantula*, *Polemonium pulcherrimum*, *Listera convallarioides*, *Senecio triangularis*, *Ribes* sp., *Washingtonia obtusata*, *Lonicera involucrata*, *Pedicularis racemosa*, *Mitella pentandra*, *Epilobium saximontanum*, grasses, and *Equisetum arvense*. A single plant of *Equisetum* was found on a log of D8 where run-off occurred during rains. There was no indication of any permanent moisture supply and the condition was still xeric.

The chart (fig. 3) indicates the similarity and differences of the successions as described above. In each station the oldest logs (D8) contain vegetation which blends with that of the surrounding forest floor, thus indicating the completion of the succession.

SUMMARY

A successional study of 153 decaying fallen logs of spruce and fir was made in the Gothic Natural Area of the Gunnison National Forest, Colorado. The logs were located in mesic, bog,

and xeric habitats, and were grouped into eight decay classes.

Fallen logs are invaded first by lichens and liverworts. These are followed by mosses with *Brachythecium* the common genus in all three conditions. Succession is continued with an herbaceous stage which varies as to species in the different habitats. In some forms the typical *Vaccinium* or low shrub stage is the next phase before the completion of the succession into the climax forest. The establishment of seedlings of the spruce and fir trees is not dependent upon this succession but can occur on logs showing only slight signs of decay. Separate successional studies in each area show a basic similarity to the general pattern.

HERBERT A. McCULLOUGH

DEPARTMENT OF BIOLOGY,
HOWARD COLLEGE,
BIRMINGHAM, ALABAMA

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A NEW VEGETATION MAP OF MANCHURIA

Manchuria is of considerable interest to students of biogeography on account of its contrasting types of vegetation and the relation of these types to the vegetation in other parts of the north temperate zone, especially sections of the United States. Much of the natural vegetation of central and southwestern Manchuria has been destroyed, and this is especially true of the plains of the Liao ho in the south and their continuation to the middle Nonni and the middle Sungari rivers in the heart of the country. The mountains, too, have witnessed much destruction, mainly in the foothills, but considerable remains of the original cover permit one to reconstruct the natural vegetation of Manchuria.

The results of recent investigations have been assembled on a new map which is here submitted for the first time (fig. 1). This map is the outcome of the cooperative efforts of the writer and of Professor M. Takenouchi, den-

drologist and professor of botany at the University of Changchun, Manchuria. The authors feel that this map expresses the present status of our knowledge of the distribution of the natural vegetation of Manchuria. However, they are fully aware of its imperfections and they in no way consider this map final. It is much rather their expressed hope that this new map will stimulate their colleagues to further investigate this important aspect of Manchurian research. This map simply brings up-to-date our incomplete information and represents a basis on which to erect a structure of more detailed knowledge. It ties up well with the best vegetation maps of the surrounding areas, especially the Korean map by Lautensach ('41) and the map of the U.S.S.R. in the Great Soviet Atlas (U.S.S.R., '37).

The map is based on the latest method of presenting vegetation: the Geographic System

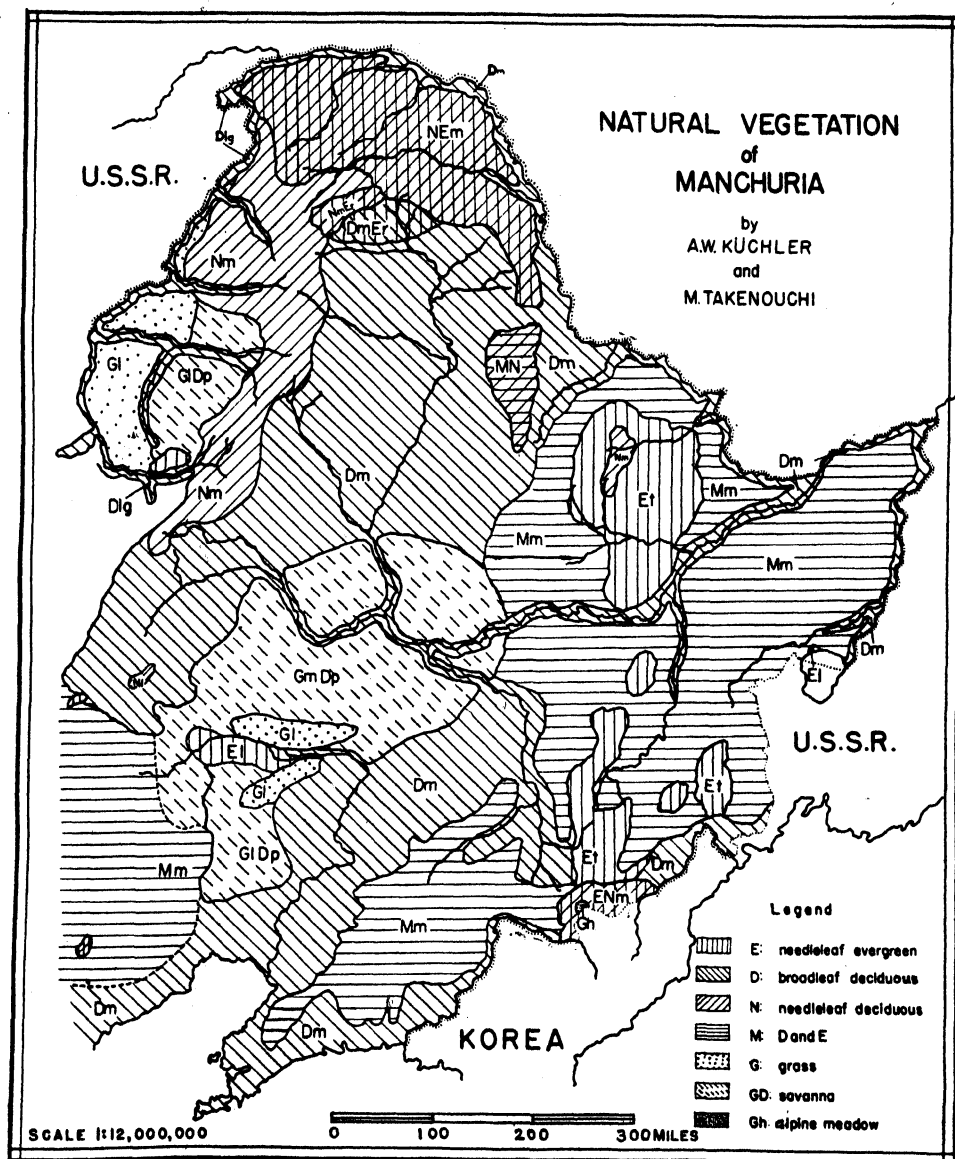


FIGURE 1.

of Vegetation (Küchler, '47) and a key to the map may be found at the end of this paper. The Geographic System of Vegetation is based entirely on physiognomy and the types of vegetation shown on the map are therefore all physiognomic types. There is therefore no reference to floristic aspects which have been dealt with elsewhere (Katigawa, '39; Takahashi, '44; Takenouchi, '41). A few remarks about the natural vegetation of Manchuria may appropriately accompany the new map.

The number of arborescent species composing the forest is very great in the southeast of the country, especially in the mountains northwest of the Korean border. This wealth continues northeastward from the valleys of the Yalu and the Tumen rivers along the Korean border to the plains of the lower Ussuri and the lower Sungari in eastern Manchuria. According to Dr. Takenouchi, the composition of the forests is almost the same in the northern and the southern part of this section of Manchuria; only

two tree species (*Taxus cuspidata* and *Abies holophylla*) which occur in the south, are absent in the northeast.

In a general way, the number of species decreases from the southeast toward the northwest. Although there is an appreciable variety of tree species in the Great Khingan Mountains in the northwest, there are also large areas covered with little more than larches. Birches form more or less prominent admixtures locally, and at times completely dominate the vegetation.

The effect of increasing latitude on the climate is reflected in the height of the trees. While the southeast possesses large areas with tall conifers, these never exceed medium height in the north.

It is not difficult to correlate the vegetation with the topography. As conifers evergreen (E) and deciduous (N) are generally the harder types of tree, they dominate the landscape in the higher altitudes. On the same basis, the broadleaf deciduous trees (D) are most prominent in the lowlands of the south and on the southern slopes and foothills of the Great Khingan. But not everywhere is there a zone of mixed forests (M) to form a transition between the broadleaf and the needleleaf forests. Such mixed forests occur on a large scale in the southeastern part of Manchuria and represent some of the most beautiful forests in the world, combining aspects of the coniferous forests of western Washington and Oregon with aspects of the great broadleaf deciduous forests of eastern North America. In addition to many typically oriental species, these mixed forests contain such familiar genera as oak, maple, linden, walnut, elm, ash, birch, poplar, willow, cherry, spruce, fir and larch, with an impressive fauna of Siberian tiger, bear, wapiti, and many others. The broadleaf deciduous forests are not only very common in the southern part of the country; they develop a strong tendency to form galeria forests¹ wherever the rivers flow through a vegetation not of this type. At one place they extend, perhaps somewhat surprisingly, in a rather broad front in the north and northwest of the Little Khingan all the way to the Amur River.

In the northwestern part of Manchuria, west of the Great Khingan Mountains, deciduous trees again form galeria forests and also spread over parts of the western grasslands to form savannas. Climatic conditions are here too severe, i.e. too arid, to permit a continuous forest cover. The galeria forests as well as the savanna trees are characterized by low stature; even species which appear as tall forest trees southeast of the Great Khingan occur often as no more than shrubs in the northwest. On the other hand, it is note-

worthy that the Mongolian grasslands do not reach far east beyond the Manchurian border before they turn into savannas. The grasses are all low in stature.

Elsewhere in Manchuria, the natural grasslands are less extensive than has been supposed in the past. In the great central plains, the grasslands are ringed by forests on all sides including the south. It is noteworthy that these grasslands are savannas, with an unexpected contrast between the northern and the southern section; the grasses are *taller* in the north. This indicates that the precipitation, decreasing as it does with increasing distance from the Yellow Sea, is more than compensated by a smaller vapor pressure deficit in the northern section. Only two relatively small areas in the grassland are not of the savanna type and lack trees entirely. The reason is edaphic and one finds here nothing but short grasses growing on a sandy soil. The sand occurs frequently in dune form and corresponds to what the Chinese call Shamo in Mongolia, in the Gobi "Desert." In Manchuria, such grass covered dune country is called Mangha, a term of Mongolian origin.

Besides the great central Manchurian grasslands there are numerous meadows in the higher elevations of the southeastern mountains. The meadows are too small to be shown on the map but occur frequently enough to be mentioned here. They are rich in non-graminaceous herbs with numerous brightly colored flowers.

Only in one region is there a development of a true alpine meadow, i.e. a meadow distinctly above timberline. It occurs approximately at the center of Korean border, on the Bakdusan, and is characterized by a dominance of forbs over grasses; it is sufficiently extensive to appear on the map.

The splendor of the natural vegetation of Manchuria, especially in the southeastern section, calls urgently for some form of conservation and preservation together with game reserves of adequate size. The ever-increasing number of immigrants is slowly but steadily pushing back the forests and the time is not far distant when the better part of these magnificent forests is destroyed.

Here follows a key to the formulas used on the new map of the natural vegetation of Manchuria; for full details concerning the Geographic System of Vegetation see Kücher ('47).

- Dlg: low broadleaf deciduous forests along rivers.
- Dm: medium high broadleaf deciduous forest.
- Dmg: medium high broadleaf deciduous forest along rivers.
- DmEr: medium high broadleaf deciduous forests with occasional evergreen needle-leaf trees.

¹ A galeria forest is a forest limited to the immediate vicinity of water courses, usually in grasslands; it owes its existence to additional soil water provided by seepage from the river.

- Et: tall evergreen needleleaf forests.
 ENm: medium high forest of evergreen needleleaf and deciduous needleleaf trees.
 El: low evergreen needleleaf forest.
 Gl: short grasses.
 GmDp: medium high grasses with broadleaf deciduous trees scattered singly or in groves.
 GlDp: short grasses with broadleaf deciduous trees scattered singly or in groves.
 Gh: meadows mostly of herbaceous plants other than grasses.
 Mm: medium high mixed forest composed of broadleaf deciduous and needleleaf evergreen trees.
 MN: mixed forest of broadleaf deciduous needleleaf evergreen and needleleaf deciduous trees.
 Nl: low needleleaf deciduous forest.
 Nm: medium high needleleaf deciduous forest.
 NEm: medium high needleleaf deciduous and needleleaf evergreen forest.
 NmEr: medium high needleleaf deciduous forest with occasional needleleaf evergreen trees.

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 A. W. KÜCHLER
 DEPARTMENT OF GEOLOGY & GEOGRAPHY,
 UNIVERSITY OF ROCHESTER,
 ROCHESTER, NEW YORK

THE USE OF THE PUNCHED CARD METHOD IN PHYTOSOCIOLOGICAL RESEARCH

References to the use of the Punched Card Method in phytosociology are practically nonexistent. Workers in other fields have pointed out the value of this method in any work involving the compilation of large quantities of data such as those obtained from a quadrat study of vegetation. The method is of great value in statistical work, and the present trend in the evaluation of phytosociological data is toward making greater use of statistical methods. Ashby ('35), Cole ('46), Dice ('45), Fracker and Brischle ('44), Stewart and Keller ('36), and others have experimented with the application of statistical methods to plant and animal relationships. Their work demonstrates the value of the statistical approach to phytosociology. The conclusion is inevitable that future research in this field will make greater use of statistical methods. These methods necessitate a considerable increase in the amount of tabulation and calculation that must be performed, and it is here that punched cards can do much to decrease the labor and increase the accuracy of the operations.

The use of Hollerith Punched Cards is common in many phases of business and research and the consequent availability of the machines to process them makes them a tool well worth the consideration of any ecologist. They are the

familiar 7% in. by 3¼ in. cards used by the post office as postal notes and by some federal agencies as checks. They have 80 columns with 10 numbered rows to a column and space for 2 additional punches in each row above the 10 numbered rows. Each row in each column can be punched, and there are therefore 960 places in which values may be inserted.

A quadrat study of an oak woods in Southwestern Wisconsin will be used to illustrate some of the uses that can be made of these cards. The study was made in the summer of 1946 and followed, with some modifications, the procedure used by Daubenmire ('36). One hundred quadrats in a 10 × 10 place grid were used; the data from each quadrat were coded and punched on a single card. A portion of the code used is shown in table I. In addition to the quadrat designation, it was possible to punch data on the 66 most important species, including three different size classes for each of the tree species. Eight tree species and all the shrub and herb species with a frequency of more than 1 were included. Space was also available for several of the shrub and herb species with a frequency of only 1, and those species considered to be the most important were included.

The method of punching these data from the code shown in table I is largely self explanatory.

TABLE I. *A portion of the code used to record quadrat data from Stewart's Woods on punched-cards*

Quadrat designation

Column 1—quadrat letter

Row 0—A
 1—B
 2—C
 3—D
 4—E
 etc.

Column 2—quadrat number

Row 0—10
 1—1
 2—2
 etc.

Tree species

Column 3—white oaks less than 2 inches DBH

Row 0—1 tree per quadrat
 1—2-3 trees per quadrat
 2—4-6 trees per quadrat
 3—7-10 trees per quadrat
 4—11-16 trees per quadrat
 etc.

Column 4—white oaks from 2-8.9 inches DBH

Row 0—10 trees per quadrat
 1—1 tree per quadrat
 2—2 trees per quadrat
 etc.

Column 5—white oaks 9 inches DBH and over

Row 0—10 trees per quadrat
 1—1 tree per quadrat
 2—2 trees per quadrat

Columns 6-22—remaining tree species coded in the same manner as for the white oaks above

Shrub species (Columns 23-42)

Column 35—*Rubus allegheniensis*

Row 0—1 individual per quadrat
 1—2-3 individuals per quadrat (number classes the same as for white oaks less than 2 inches DBH)

Herbaceous species (Columns 43-80)

Column 52—*Circaea latifolia*

Row 0—1 individual per quadrat
 1—2-3 individuals per quadrat (number classes the same as for white oaks less than 2 inches DBH)

individuals, and row 9 was used to designate that the quadrat had from 145-274 individuals. It was thought that a sliding scale would be especially valuable since many of the species occur in only small numbers, and the difference between 1 individual per quadrat and 10 individuals per quadrat may be highly important. In the case of other species, for example, *Rubus allegheniensis*, commonly a large number of individuals are present per quadrat and the difference between 25 and 50 individuals is no more important than the difference between 2 and 5 individuals of a less abundant species. Were equal number classes to have been established, the size of the classes would have been about 25 individuals per class. Some of the species never had more than 10 individuals per quadrat, and consequently they would have appeared in only the first number class.

The machine used to count and sort these cards sorts at the rate of 400 per minute. It sorts 1 column at a time, and throws the cards into 13 pockets, 1 pocket for each of the 12 rows in the column and 1 pocket for those cards having none of the rows in the column punched. A tabulating device records the number of cards thrown into each pocket, and gives subtotals and totals. The data from which are computed frequency, density, and abundance are taken directly from the dials of the tabulator. Frequency may be obtained by adding the number of cards thrown into each of the pockets corresponding to the number classes used, or more simply by subtracting the number of cards on which the species was not present from the total number of cards. A method of obtaining the approximate total number of plants of each species present in the quadrats for computing density and abundance is to multiply the number of cards in each number class by the midpoint of the class and add the products. The use of this method results in figures for the less abundant species that are very close to the true figures, while the more abundant species show a wider variation. *Adiantum pedatum*, with a fairly high abundance of 40.5 and a density of 81, had an abundance of 37.5 and a density of 75 computed by the method outlined above. *Geranium maculatum*, with a true density of 459, had a density of 468 by the above method. *Galium concinnum* had a true density of 884 and a computed density of 960.

From the standpoint of obtaining frequency, density, and abundance data, the use of punch cards results in a considerable saving of time. Tabulation of the raw data from a hundred quadrats by hand and the subsequent additions and divisions necessary to obtain the final figures normally consume the spare time of the ecologist for weeks or even months. The time required by a completely inexperienced operator to punch the 100 cards used in this study was 4 hours. An

tory, but will be reviewed briefly. The designation of quadrat D 4 is recorded by punching row 3 in column 1 and row 4 in column 2. If the quadrat contained 7 white oaks less than 2 inches DBH, row 3 in column 3 was punched. If it contained 2 white oaks between 2 and 8.9 inches DBH, row 2 in column 4 was punched. The same procedure was followed for all the other tree species. For the shrub species, and herb species, the column designated in the code for that species was punched. Since there were often more than 12 individuals of a single species in a quadrat, it was necessary to establish number classes for the shrubs, herbs, and trees less than 2 inches DBH. A sliding scale was used. Row 0 was used to designate that the quadrat contained 1 individual, row 5 was used to designate that the quadrat had from 17-26

experienced operator could undoubtedly punch the same number of cards in an hour or less. The cards were checked for errors by hand, and the ones found to be in error were re-punched. The total time required to punch, check, and re-punch the cards found to be in error was less than 10 hours. This work is purely mechanical and should be performed by an experienced punch card machine operator, who could do the work in a fraction of the time. The time required to run the cards through the counting and sorting machine was very small. At 400 cards per minute, the entire 100 cards could be counted and sorted for any column in 15 seconds. To this must be added the time required to record the data and place the cards back in the machine, but the entire time required to sort the cards and tabulate the results for every column was less than 2 hours.

The saving of time resulting from the use of the punched card method in determining frequency, density, and dominance data is sufficient to justify its use, but this is only the first of many uses. It is possible to sort the cards for a single species, and then re-sort the cards containing that species to determine the other species occurring in the quadrats with it, and their frequency of occurrence and density. From these figures it is possible to make the chi-square test of independence and association and to run correlations on the relationship between the den-

sity of one species and any other. In the quadrat study mentioned above, chi-square tests (Dice, '45) were run on the association of each species having a frequency of 20 per cent or more with every other species having a frequency of 20 per cent or more. The results for those species showing a significant degree of deviation from the amount of association that would be expected from a random distribution are shown in table II. An analysis of these results has been presented elsewhere (Cottam, '48) and will not be repeated here. The value of these data in phytosociological studies is evident, but the great amount of time required to compile such a table using manual methods is prohibitive. A total of 191 different associations of one species with another was made, of which the table represents only those species showing significant deviations from the degree of association that would be expected from a random distribution with at least 4 species. The time required manually to extract from the raw data the number of times 191 different combinations of 2 species occurred together cannot be estimated, but would certainly be more than the results would normally justify.

The uses made of the Punched Card Method in this study are only simple examples of what can be done with the proper equipment and an adequate understanding of its capabilities. Machines are available that will print the data

TABLE II. Association of selected species

| | <i>Parthenocissus vitacea</i> | <i>Rubus occidentalis</i> | <i>Amphicarpa bracteata</i> | <i>Circaea latifolia</i> | <i>Desmodium acuminatum</i> | <i>Galium concinnum</i> | <i>Geranium maculatum</i> | <i>Osmorhiza Claytani</i> | <i>Phryma leptostachya</i> | <i>Pteridium aquilinum</i> | <i>Quercus</i> seedlings | <i>Prunus</i> seedlings | <i>Amelanchier interior</i> |
|-------------------------------|-------------------------------|---------------------------|-----------------------------|--------------------------|-----------------------------|-------------------------|---------------------------|---------------------------|----------------------------|----------------------------|--------------------------|-------------------------|-----------------------------|
| <i>Parthenocissus vitacea</i> | | + | | | ++ | + | | ++ | | - | - | - | - |
| <i>Rubus occidentalis</i> | + | | | + | | | | ++ | | | - | | |
| <i>Amphicarpa bracteata</i> | | + | | | ++ | + | | | + | | - | | |
| <i>Circaea latifolia</i> | | | | | ++ | | | ++ | + | | - | | |
| <i>Desmodium acuminatum</i> | ++ | | ++ | ++ | | ++ | ++ | | ++ | - | - | | - |
| <i>Galium concinnum</i> | + | | + | | ++ | | ++ | | | - | - | | |
| <i>Geranium maculatum</i> | | | | | ++ | ++ | | | | - | - | | |
| <i>Osmorhiza Claytani</i> | ++ | ++ | | ++ | | | | | | - | - | | - |
| <i>Phryma leptostachya</i> | | + | + | + | ++ | | | | | | - | - | - |
| <i>Pteridium aquilinum</i> | - | - | | - | - | | - | - | | | | | |
| <i>Quercus</i> seedlings | - | - | - | - | - | | - | - | | | | | + |
| <i>Prunus</i> seedlings | - | | | - | - | | - | - | | | | + | + |
| <i>Amelanchier interior</i> | - | - | | | - | | | - | - | | | | |

The plus signs indicate that the degree of association between the two species concerned is significantly greater than that expected from a random distribution. The minus signs indicate that the degree of association is significantly less than that expected from a random distribution. The single symbol indicates that the probability of achieving a greater chi-square value with a random distribution is less than one in 20. The double symbol indicates that the probability is less than one in 100.

obtained from the cards, multiply, give sums of squares and sums of products. Much of the computations as well as the actual sorting and counting can be performed on the machines. The use of this method in phytosociology is practically limitless.

The most important principle to be considered in the use of this method is the necessity for establishing some kind of a code. In the work just reviewed the punch card method was not considered until the raw data had been gathered and most of it tabulated. This necessitated going over the raw data to code the results. Some of the raw data were not obtained in a manner best suited for their being placed on the cards. Any study contemplating the use of these cards should be carefully evaluated before any of the data are gathered. It should be decided what results will be wanted and how they should be expressed. The code should be set up before the workers enter the field, and the initial data should be recorded according to the code, so that the cards may be punched from the raw data without the necessity of a coding operation. This will not only save considerable time, but will reduce errors. In addition, setting up the study so that it can be evaluated with the assistance of punched cards will result in a better organization of the study.

References that will be of value to anyone contemplating the use of this method are those of Hartkemeier ('42), which is a handbook explaining the principles of operating the machines, and Bachne ('35), which is a series of articles written by workers in a variety of fields explaining the applications of the punched card method to their particular specialty.

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GRANT COTTAM

UNIVERSITY OF HAWAII,
HONOLULU, T. H.

J. T. CURTIS

BOTANY DEPARTMENT,
UNIVERSITY OF WISCONSIN,
MADISON, WISCONSIN

A RANGE SOCIETY FORMED

A new society for professional range men, pasture specialists, graziers, ranchers, and range users held its first annual meeting at Salt Lake City on January 30 and 31, 1948. The second annual meeting is to be at Denver in late January or early February 1949.

The purpose and objectives of the society are:

1. To foster advancement in the science and art of grazing land management.
2. To promote and support the maximum sustained use of forage and soil resources of the nation's grazing lands.
3. To stimulate discussion and understanding of practical range and pasture problems, and provide a medium for the exchange of ideas and facts among members and with allied workers.
4. To encourage professional improvement of its members.

Membership in this new range society is open to all persons engaged in or interested in range or pasture management. These liberal membership requirements reflect the broad training needed in the field of range management. The nearly 600 members represent the livestock industry, colleges and universities, federal, state, and other agencies.

This society arose as a result of the desire of workers in the field for an organization where they could exchange ideas, discuss and agree upon procedures and practices, and, in general, further the maintenance and improvement of the grassland resource. They felt that the forage resources which cover over one-half the total land area of the United States need greater emphasis because of their importance as one of our basic natural resources.

The society has as one of its goals the publication of a journal treating with range and pasture problems. It is hoped that the first issue of this journal will be released during 1948.

The present officers of the society are: President—Joseph F. Pechanec, Portland, Oregon; Vice-President—W. T. White, Portland, Oregon; Secretary-Treasurer—Harold F. Heady, College Station, Texas; Council Members—

F. G. Renner, Washington, D. C.; George Stewart, Ogden, Utah; L. A. Stoddart, Logan, Utah; D. F. Costello, Fort Collins, Colorado; B. W. Allred, Fort Worth, Texas; and Vernon A. Young, College Station, Texas.

HAROLD F. HEADY .
AGRICULTURAL AND MECHANICAL COLLEGE OF
TEXAS,
COLLEGE STATION, TEXAS

BOOK REVIEWS

MERRILLEANA ¹

Too often in the press of teaching and research we tend to limit our reading to our own narrow specialties—and we come to accept our colleagues on the basis of established reputation, rather than by evaluating them through careful reading of their published work. Especially is this likely to be the case when the colleague in question is labelled with a tag which places him arbitrarily in another sector of the biological garden. Thus Dr. Merrill may with propriety,—but what a narrow propriety!—be labelled *taxonomist-administrator*. This is illustrated by selection of the well-chosen series of papers which that sympathetic editor-botanist, Frans Verdoorn, has selected for us from among the extensive writings of Dr. Merrill. It is true that many of his publications deal with taxonomy in its more esoteric phases and others with by-products of his administrative experience. But included in this skillfully selected series are examples of papers in two fields which are of interest to many an ecologist—the one, plant geography,—the other, plants in relation to man.

The first of the phytogeographical papers reprinted in "Merrilleana" dates back to 1907 and in it Merrill describes his ascent of Mount Halcon, Mindoro, in the Philippines. We are reminded in this paper that Merrill's understanding of phytogeographical problems is based on sound field experience and on an ability to record his observations convincingly. In this paper we also see an early manifestation of his interest not only in man for his own sake but also in the relation of man in his natural state to the plants he uses for food and shelter, as described in this case for the Mangyans. Nor, in this early paper, is there lacking an awareness of the significance of Mangyan land-use from the point of view of conservation. An essay "On the flora of Borneo," extracted by the editor from Merrill's "A bibliographic enumeration of Bornean plants" (1921), also makes good reading; it is followed by a reprint of "Die pflanzengeographische Scheidung von Formosa und den Philippinen" (1923). We come then to another essay, "Correlation of the indicated biologic alliances of the Philippines with the geologic history of Malaysia," extracted from Merrill's "An enumeration of Philippine flowering plants" (1926),—here we have a clear and detailed discussion of the phytogeographic problems of the areas which led to the establish-

ment of the modified concept of Wallace's Line, now often referred to as the Wallace-Merrill Line, and a consideration of the relation to it of Weber's Line,—all in the light of biological-geological information. The phytogeographer and anthropologist both will enjoy the brief article "Scuttling Atlantis and Mu"—scuttled indeed with a heavy lading of Indian corn, squash, pumpkin, cherimoya, tobacco, llama, Muscovy ducks, and other assorted biological miscellanies!

Of Merrill's papers on plants in relation to man—ethnobotany, if you will,—the first reprinted is "Comments on Cook's theory as to the American origin and prehistoric distribution of certain economic plants, etc." (1920), in which botanical and philological arguments and facts are brought into play in the service of the anthropologist. The content of other papers of more or less the same general interest is indicated by their titles—"On the significance of certain Oriental plant names in relation to introduced species" (1937), "Domesticated plants in relation to the diffusion of culture" (1938), "Man's influence on the vegetation of Polynesia, with special reference to introduced species" (1941), and perhaps peculiarly apt because the author is himself a smoker, "Further notes on tobacco in New Guinea" (1946). Fortunately the bibliographies of these papers have been included in their re-printing.

"Merrilleana" is complete with title-page, editor's foreword, pertinent illustrations and portraits, table of contents, an "*illustrissimi auctoris vita*," and a bibliography of some 488 titles published from 1899 through 1946. Tastefully executed vignettes representing plants named for Dr. Merrill appear here and there throughout.

It is indeed encouraging that the gracious custom of gathering together the important and varied publications of our leading scientists continues² in spite of shortages of paper and high printing costs. Thus, we may not only honor those who have achieved eminence, but we are also provided with the opportunity to re-survey the foundations upon which that eminence has been built; and, as in the case of "Merrilleana," we are also afforded an opportunity to view new facets of their scientific personalities.

E. C. ABBE

DEPARTMENT OF BOTANY,
UNIVERSITY OF MINNESOTA,
MINNEAPOLIS, MINNESOTA

¹ Verdoorn, Frans, editor. 1946. *Merrilleana*. A selection from the general writings of Elmer Drew Merrill, Sc.D., LL.D. *Chronica Botanica*, vol. 10, No. 3/4, pp. 127-394. 23 illustr. Separately issued at \$4.00.

² Compare also in this connection, Oakes Ames. *Orchids in retrospect—a collection of essays on the Orchidaceae*. Botanical Museum of Harvard University. 1948.

A SOCIOLOGIST LOOKS AT THE "KINSEY REPORT"¹

The Kinsey report is rightfully a scientific contribution of high order. It presents a vast compilation of data for an area that has been essentially "terra incognita." Our knowledge of human sexual behavior is characteristically unsatisfactory, largely because of the social myth, ethical injunction and personal conjecture which pass as established fact. Dr. Kinsey and his associates have simply dug out, amassed and arranged an immense amount of data on one feature of sexual behavior. These data necessitate a radical replacement of myth and conjecture and they fill in a significant void in our factual knowledge of human life. It is in this sense that the Kinsey report is a momentous scientific contribution. The report is also of distinct significance in outlining and giving status to taxonomic inquiry into social life on an extensive scale and on a systematic basis. The extension of the Kinsey procedure to other facets of social life—such as ambition, honesty, opportunism, habits of drinking, friendship, enmity, and anxiety—would yield realistic information sorely needed in social science.

The outlines of the Kinsey study are simple. The present book is based on interview material on sexual behavior secured from some 5300 white males of the United States and Canada. This group of males is broken down into classes so as to yield homogeneous samples for marital status, age by five year periods, educational level, rural-urban background, and religious background. This breakdown yielded 698 samples available for comparison on sexual behavior. The criterion of sexual behavior which is used is the act of orgasm. Two primary items of information are secured: (a) the incidence of use of the *type* of sexual outlet and (b) the frequency of orgasm. The types of sexual outlet considered by the authors are masturbation, nocturnal emission, homosexuality, petting to climax, coitus (pre-marital, marital, extra-marital and post-marital), and animal contacts.

The arrangement of the information on incidence and frequency of sexual outlet, according to the sample breakdowns, yields a voluminous number of findings. Most of these findings are significant. Many are spectacular. For the benefit of those who have not read the report a few of the interesting findings may be mentioned.

The average frequency of orgasm for the entire white American male population up to the age of 85 is 2.34 times per week. For

those below 30 years it is 3.27 per week. There is an enormous range in variation from one who has had only one orgasm in 30 years to those who have thirty a week. Seven and six-tenths per cent of the white male population have daily sex outlets.

In the total male population, single and married, between adolescence and old age, 24 per cent of the total outlet is derived from solitary sources (masturbation and nocturnal emission), 69.4 per cent is derived from hetero-sexual sources (petting and coitus), 6.3 per cent of the total is derived from homo-sexual contacts, and 0.3 per cent is derived from relations with animals of other species. Although marital intercourse is the chief medium of sex outlet it does not provide even half of the orgasms of the white male population.

For males of lower level groups 80 per cent of sex outlets during the early years of marriage are through marital intercourse. This increases to 90 per cent by the age of 50 years. For males of the college level 85 per cent of sex outlets come through marital intercourse during the early years of marriage; for this group at the age of 55 no more than 62 per cent of sex outlets come through marital intercourse.

"... it is probably safe to suggest that one-half of all married males have intercourse with women other than their wives, at some time while they are married." (P. 589.)

At least 37 per cent of the white male population has some homo-sexual experience between the beginning of adolescence and old age. For 35.8 per cent of the single males in the 26-30 year age group homosexuality is one form of outlet.

Between 92 and 97 per cent of the male population have engaged in masturbation. In the college male group two-thirds of total sex outlets prior to marriage are through masturbation.

In the age period 16-20 years, 85 per cent of the males who have not gone beyond the eighth grade engage in pre-marital intercourse. Of the college group in this age period, 42 per cent engage in pre-marital intercourse.

The patterns of sex behavior established by the age of 16 tend to persist throughout the life of the individual.

In the light of such illustrative findings it is easy to understand the great concern that has been aroused over the soundness of the method and findings of the Kinsey report. This concern becomes primarily a matter of assessing (a) the validity of their interview material and (b) the adequacy of the sample.

To one with extensive experience in interviewing human beings on delicate matters it is apparent that the interview procedure used in the current study is of a high order of com-

¹ Kinsey, Alfred C., Wardell B. Pomeroy, and Clyde E. Martin. 1948. Sexual behavior in the human male. Philadelphia: W. B. Saunders Co. Pp. xv + 804. \$6.50.

petency. The authors' specifications with regard to establishing contact, inducing rapport, preserving confidence and opening the channels of frank disclosure bespeak sophisticated, skilled, and wise interviewing. However, even the most skilled and wise interviewing does not assure valid replies. Deficiencies of memory, improper motivations, tendencies to exaggerate or minimize, reservations in revealing information of a self-incriminating nature and unfortunate moods of both questioner and respondent at the time of the interview may seriously distort the validity of replies. The authors have employed a number of checks which give reasonable assurance of the general validity of the information they have collected. These were (1) a series of retake interviews after an interval of approximately three years, with comparison of incidence of sexual outlet and frequency of sexual outlet yielding coefficients of correlation of 0.9 and 0.6 respectively; (2) similarity of replies of spouses on matters in which both were involved; (3) internal consistency of the interview replies; (4) similarity of the findings of those belonging to the same statistical cell; and (5) the closeness of findings between successive samples of groups on which complete coverage (100%) was eventually secured. While these tests of validity do not cover all items they are sufficiently significant to impart reasonably high probability to the general validity of the interview responses.

Most of the intelligent criticism of the Kinsey report has centered on the adequacy and quality of the samples employed. Dr. Kinsey's study is taxonomic and thus requires a good representative sample of the entire population. Further, since he indicates that his primary interest is in segments of the population rather than in the whole population adequate samples of such segments are required. There can be no question that the samples used in the report differ considerably in adequacy of size—differences which are not made clear in the presentation of the compiled data since figures on incidence and frequency from good sized samples and from questionably sized samples are placed side by side without identification of the matter. However, while statistical weakness of this sort exists it is highly doubtful that it affects much the general reliability of the data. Comparisons of the findings from partial samples with those from the largest inclusive sample show no major variations. In the judgment of this reviewer technical weaknesses of the size of some of the samples do not throw any serious doubt on the general soundness of the Kinsey findings.

Questions have been raised concerning the quality of Dr. Kinsey's sample, primarily with regard to its selective nature. The individuals in the sample were volunteers. It has been

charged, consequently, that these individuals constituted a biased group. While this charge might seem reasonable on a *a priori* grounds it appears to have little substance in the light of different comparisons of the data. The most significant point to be noted is that in the groups over which in time Dr. Kinsey has been able to secure complete coverage, no appreciable differences are found between the information secured from the initial batches of volunteers and the later batches of recalcitrant individuals whose cooperation was secured only through persistent solicitation and through social pressure of the local community. In the light of such findings the *a priori* charge of a biased sample loses much of its weight, so far as the kind of information sought is concerned.

It must be readily admitted that the data collected by the authors are not perfect, because of deficiencies in sampling and because of imperfect control over matters that distort the validity of interview replies. However, a fair and reasonable assessment of the work of the authors must lead one to recognize that these deficiencies are minor in significance and affect only the fringe bands of the data. It may be noted that the authors are aware of the necessary limitations of their data, stating on page 153, "... it should be ... recognized that the data are probably fair approximations, but only approximations of the fact." Fair approximations to the facts is about all that can be expected from a pioneering incursion into a vast, complicated and secretive area of collective conduct. This reviewer strongly suspects that the major findings of the present report will not be changed significantly by the further information secured by the authors as they reach their goal of 100,000 case histories of the American population.

To a sociologist the weakness of the Kinsey report as a contribution to our understanding of the sexual behavior of the American white male population is its inability to specify the social character of the instances and patterns of sexual outlet. This is no criticism of the authors since their problem and their plan of attack compel them in major measure to ignore or pass by the social meaning of sexual outlets. The act of orgasm which the authors use as the criterion of sex outlet is a mere biological occurrence. In actual life it is situated, so to speak, in a framework of social definition and social practice which constitute the realistic nature of sexual behavior as a part of social life. To use the instances of orgasm as identical counters, to be grouped statistically in a very formal and highly abstracted framework of census categories, yields a biological picture of diversified distribution, but a picture which obscures and distorts the nature of sexual occurrences in the social life of the individual

and the group. Consequently, to regard the findings of the Kinsey report not solely as a picture of the quantitative distribution of a common biological item but instead as an account of the social form of sexual behavior is to read into the report a content which it just does not possess. And this is precisely what readers will do, especially since no deterring cautions are presented in the text and since the authors, themselves, are prone to do this very thing.

The meaning of my remarks can be made more understandable through a few illustrative references. Thus, in their consideration of homosexuality the authors, by necessity of their procedure, treat this form of outlet as identical in all instances, merely differentiating between census categories in terms of the incidence and frequency of this outlet. Yet, homosexuality has a profoundly different social nature as between its occurrence as a casual episode in the life of a fifteen year old farm boy and its occurrence in a thirty year old habitué of an urban homosexual cult. A similar profound difference in social nature and meaning exists in the case of extra-marital sexual outlet, as between the temporary resort thereto by a husband because of the protracted absence or illness of his wife and the rooted practice pursued by social sets of married couples in some communities, of circulating freely and regularly among each other in their sex contacts. These two illustrations (which can be matched for every other type of sexual outlet dealt with by the authors) suggest the significant diversification in the social nature of sexual behavior which is completely "swallowed-up" in the authors' unit figures on incidence and frequency. We simply do not know from these figures what is their social nature

and meaning—all we have is a count of the biological occurrences of orgasm. We do not know, among other things, whether or in what degree the instances of sexual outlet represent transitory experiences, unstabilized occurrences, immature organization, breakdowns of control, stabilized group practices or steady and studied rebellion to a code.

I recognize clearly that such knowledge of the social nature of sexual behavior was not part of the research objective of the authors and, indeed, that it is largely precluded by the very taxonomic method which they employ. Yet the way in which their work is bound to be received, freely abetted by their own manner of interpretative treatment, implies a social depiction of sexual behavior whereas the study can present actually only a picture of the quantitative distribution of the physiological act of orgasm. The difference between these two matters is not trivial nor a forced instance of special pleading. It is basic to an understanding of the meaning of the authors' study as a body of fact to be brought inside a realm of scientific knowledge. The difference is also basic to an understanding of the implications of the study. The authors have correctly recognized that their findings may or should have important consequences for law and regulative institutions, for counselling and clinical practice and for readjustments in social norms and conceptions. Yet, the derivation of principles, meanings, norms and insights from the Kinsey findings that may be safely and intelligently applied to such areas is necessarily limited because we are actually given in the findings only a biological and not a social picture.

HERBERT BLUMER

DEPARTMENT OF SOCIOLOGY,
THE UNIVERSITY OF CHICAGO

CONSERVATION IN THE UNITED STATES¹

Today, the subject of this book is in the minds of Americans more than at any time in history. Inventories of the nation's natural resources are not encouraging in their revelations, for war has been won at a great cost and has hastened the exploitation of essential products of land and water. The nucleus of this significant contribution from Cornell might well lie in the challenge it raises emphatically in the minds of its readers, namely—to conserve lest we perish. The task of fur-

thering this realization in the minds of all thinking and forward-looking Americans is an extremely difficult one, and no less important. The authors have shared in this extensive undertaking through contributions in four parts, namely: "Conservation of Soil and Water Resources"; "Conservation of Forests, Parks, and Grazing Lands"; "Conservation of Wildlife"; and "Conservation of Mineral Resources."

Part I embodies four chapters dealing with fundamental aspects of soil and land productivity, of water and its uses, of soil depletion and erosion, and lastly, of current methods for preserving normal soil conditions. The reader is given, in a direct and logical sequence, an abbreviated story of the origin, use, misuse, and productivity of major soil types. The contributing roles played by water in the production

¹ Gustafson, A. F., C. H. Guise, W. J. Hamilton, Jr., and H. Ries. 1947. *Conservation in the United States*. Comstock Publishing Co., Inc., Cornell Heights, Ithaca, N. Y. Second Edition, Fourth Printing. Pp. 477, 236 figs.

of food, power, transportation, and recreation are briefly introduced. Soil depletion and soil erosion are treated interestingly and, quite properly, an entire chapter is devoted to soil conservation. Most appropriate and effective illustrations are included. The possible need in the future for government control to assure reasonable protection and utilization of the nation's soil is pointed out. No discussion is included of the advantages and disadvantages of government control over natural resources.

Part II deals with forest, range and park areas and problems, and is presented in a forceful and authoritative manner. An unbiased story of the extent of utilization, destruction and depletion of forests is given, together with a plea for more adequate protection against fires, and for an extension of sustained management practices. In a few well-chosen paragraphs the reader is brought face to face with the basic present day needs in forest conservation and range management.

The section on wildlife conservation, especially the chapter on fish and fisheries, impresses the reviewer as being exemplary. Particularly is this discussion welcome, for all too frequently modern books in the general field of biology and conservation treat in but a cursory fashion this highly pertinent field of research. The content of the discussion is thoroughly authoritative. One oversight is noted in figure 171 in which reference is made to dredging starfish from "Lower Chesapeake Bay, Maryland." Obviously, this should read, Lower Chesapeake Bay, Virginia.

The concluding part on metals, mineral fuels, and non-metallic minerals contrasts the past with the present supplies and points out the need for conserving certain of these reserves for safeguarding the nation's independence from acute and vital shortages in future years.

The critical reader will note the omission of a discussion of the value of preserving natural populations large and small in their normal habitats for research purposes. Conservationists would benefit by having the reader's attention called to some of the particular scientific uses of undisturbed biotic areas of large extent where the ecology of species formation and animal behavior can be realized and interpreted. Frequently, the effects of the disturb-

ance of a particular economic balance can be readily measured, compensated for or overcome. Unfortunately, however, there is no substitute for an undisturbed pristine environment as a basis for understanding the effects of many natural, biological processes.

Every student of conservation is probably aware of the fact that this study is, in large measure, a population problem. Oysters, crabs or fish, as well as ducks or pronghorn antelopes, are simply different types of populations requiring individual methods of study adapted to each type. The perpetuation of these animals is dependent on a knowledge of their biology and the fundamental, specialized technics which have been devised for population analyses and predictions. The extent of their preservation and use will be influenced materially by the progress of these studies. Also, success in maintaining a sustained yield in the case of a commercial population, or in preventing the extinction of a particular species, rests in no small measure on conscientious enforcement of established laws and regulations. Here lies a great weakness in the whole conservation structure, one that needs emphasis and serious attention in every conservation education treatise. A better informed public opinion is needed.

Conservation represents more than a set of worthy ideals and of coordinate principles of human behavior in relation to beautiful landscapes and vanishing species. For accomplishing the purposes and objectives so admirably set forth in this book, conservation embodies a highly specialized branch of scientific knowledge with its own special technics and ecological methods, the development of which will most assuredly influence the conditions of life on this planet during the present and future generations.

The authors have presented a wealth of well selected, factual information in a reasonably condensed form. The book is authoritative, comprehensive, and above all readable with fine illustrations. It is recommended to every conservationist, sportsman, and lay-naturalist, and should be required reading material for every biology student.

CURTIS L. NEWCOMBE

CRANBROOK INSTITUTE OF SCIENCE
BLOOMFIELD HILLS, MICHIGAN

MAMMALS OF WASHINGTON STATE ¹

This volume contains thirteen chapters with a bibliography and index, and eighteen illustra-

¹ Dalquest, Walter W. 1948. *Mammals of Washington*. Lawrence, Kansas. University of Kansas Publications, Museum of Natural History, vol. 2, pp. 144, figs. 140.

tions of topography, forty-five of mammals, and seventy-eight distributional maps. Besides a Check List and Accounts of Species and Sub-species, comprising 305 pages, there are chapters on Physiographic Provinces, Distributional Areas, Climate and Vegetation, Life-zones and Ecology, Geologic History of Washington, The

Faunas, Speculation as to Emigrational History of the Mammals, and Speculation as to the Later Distributional History of the Mammals.

The author states that "although the principal purpose of this report is to describe and interpret the distribution of the various species and races of mammals that occur in Washington, a brief description and account of the habits of the animals is included."

In the first chapter Culver's seven physiographic provinces of Washington are named and described and in the next chapter are compared with the "Distributional Areas." These provinces and areas are not wholly identical, some provinces being divided into two areas and other provinces combined in one area. Five life zones are represented in the state, the Arctic Alpine, Hudsonian, Canadian, Upper Sonoran, and Transition, the latter being divided into the Arid-grasslands, Arid-timbered, and Humid. A table lists the mammals with their frequency of occurrence in these zones.

There is a short description of the Geologic History of Washington with a map of the extent of the Vashon-Wisconsin glacier.

The mammals of Washington are divided into three principal faunas, the Great Basin Fauna, the Pacific Coastal Fauna, and the Rocky Mountain Fauna, and the typical species for each are listed.

Speculation as to the emigrational history of the mammals is based on the extent and effect of the ice sheet. Discussion of the later distributional history is more detailed, covering all the forms, and is an interesting attempt to explain the various causes of present day distribution and the relationships between the various species and subspecies. It is based partly on the extent of the Vashon and Wisconsin Glaciers and also on the probable geographic origin

and spread of species since their retreat. The more recent invasions of such mammals as the black-tailed jack rabbit are also noted.

The Accounts of Species and Subspecies are entirely adequate. They include a general account of the species, with its common name, followed by details for the subspecies, with scientific name, synonymy, type, racial characters, measurements (external only), distribution, and remarks. Under this last heading are notes on habits, habitat, distribution, breeding, food, etc., which show the results of the author's careful field observations. A distributional map is provided for each form. Skull measurements and detailed lists of specimens with localities are quite properly omitted. A chapter on instructions for collecting would be a useful addition to the volume.

In all, 230 species and subspecies of mammals are listed, of which ten are introduced and 23 are marine forms. The 197 living native land mammals include 6 orders, 20 families, 58 genera, and 101 full species.

The marine forms are not described in detail as Victor B. Scheffer and John W. Slipp were working on an account of them that has just appeared in *The American Midland Naturalist*, vol. 39, no. 2, pp. 257-337, March 1948.

The Mammals of Washington is based on at least four years of field work from 1936-1940 and the examination of about ten thousand specimens, and the author was aided by Dr. Victor B. Scheffer who contributed his field notes, specimens, and photographs. The work is another addition to the growing list of detailed state reports on mammals and will be of use and interest to ecologists, taxonomists, and naturalists.

C. C. SANBORN

CHICAGO NATURAL HISTORY MUSEUM

INDEX TO VOLUME 29

A

- Abbe, E. C., reviews, 400, 521
 Abnormal development of tunicates attached to glass surfaces adjacent to antifouling paints, note, 215-218
 Aërial survey in forestry and agriculture, review, 222-223
 Algae, effects of, in rain-crust of desert soils, 95-100
Amphiuma tridactylum, salamander, observations on a population, 479
 Andrews, Ted F., note, 501
 Animals, desert and water-like surfaces, 391
 Annual-plant vegetation of the California foothills as related to range management, article, 72-79
 Ants of the genus *Formica*, 316
 Aquatic plant colonization on an open shoal, 205-208
 Arend, John L., note, 375-376
 Arizona, effects of algae and molds in rain-crust of desert soils, 95-100
 Arizona, mesquite seeds viable after 44 years, 393
 Arizona, perennial grass composition as an indicator of condition of southwestern mixed grass ranges, 190-204
 Autecology textbook, plants and environment, review, 398-399
 Autobiographical notes on intellectual experiences and development, 227-241

B

- Bailey, John Wendell, book notice, 131
 Barlow, Lady Nora, reviewed, 127
 Barnacles, abnormal growth and development of, 116
 Baum, Werner A., reviewed, 223-224
 Beach, Frank A., reviewed, 396
 Beall, Geoffrey, article, 80-94
 Bentley, J. R. and M. W. Talbot, article, 72-79
 Biapocrosis—method in ecology, 30
 Biotic communities and bird populations, 101
 Bird populations and biotic communities in northern Lower Michigan, article, 101-114
 Biscayne Bay, Florida, marine organisms in, 153
 Bishop, David W., co-author, article, 54-71
 Blumer, Herbert, review, 522
 Brues, Charles T., book notice, 131
 Buell, Murray F., and Robert L. Wilbur, article, 352-359
 Burbanck, Madeline P., co-author, article, 360
 Burbanck, W. D., John P. Edwards, and Madeline P. Burbanck, article, 360-367
 Burnett, Thomas, review, 130; article, 181-189
 Butterfly, *Danaus plexippus* Linn., fat content, as affected by migration, 80

C

- Cagle, Fred R., article, 479
 Cahalane, Victor H., reviewed, 129
 Cain, Stanley A., and J. V. Slater, article, 492
 California foothills, annual-plant vegetation as related to range management, 72-79
 California, germination of desert plants in the Joshua Tree National Monument, California, 242-253
 Canfield, R. H., article, 190-204
 Cantlon, John E., review, 223-224
 Carbon dioxide and fog as related to apparent photosynthetic rate of some broadleaf evergreens, 507
 Cassandra in Latin America, book review, 221
 Changes in vegetation and production of forage resulting from grazing lowland prairie, article, 1-29
 Chicago area dunes, spiders in, 334
 Clarke, George L., and David W. Bishop, article, 54-71
 Climatic change and forest sequence in northeastern North America since early Wisconsin time, 326-333
Colias, ecological segregation of inter-fertile species, 461
 Colonization of certain aquatic plants on an open shoal, note, 205-208
 Colorado, plant succession on fallen logs in virgin spruce-fir forest, 508
 Commonness, and rarity, of species, article, 254-283
 Communities, biotic, and bird populations, 101
 Comparison of two ants of the genus *Formica*, article, 316-325
 Connecticut, effects of 2,4-D in vegetation, 1947, 382-386
 Conservation in the United States, review, 524
 Contribution to the knowledge of the Pleistocene flora of Minnesota, article, 284-315
 Convection patterns in the atmosphere and ocean, book review, 128
 Cooke, Wm. Bridge, note, 376-382
 Cottam, Grant, and J. T. Curtis, note, 516
 Cowbird (*M. ater*) and the Cuckoo (*C. canorus*), note, 115-116
 Crayfish, toleration of lowered oxygen, 360
 Crombie, A. C., review, 127
 Crustaceans, marine, larval coleoptera and dip-tera from, 392
 Cuckoo and the cowbird, 115
 Curtis, J. T., co-author, note, 516
 Curtis, W. C., and M. J. Guthrie, book notice, 131
 D
 Dalquest, Walter W., reviewed, 525
Danaus plexippus Linn., fat content as affected by migration, 80
 Darland, R. W., co-author, article, 1-29

- Darwin and the "Beagle," book review, 127
 Darwin's finches and evolution, book review, 219
 Daubenmire, R. F., reviewed, 398-399
 Davis, David E., article, 437
 Dendrometers, dial gauge, 208
 Density, population and frequency index relationship, 389
 Desert plants, observations on germination in the Joshua Tree National Monument, California, 242-253
 Desert soils, effects of algae and molds in rain-crust, 95-100
 Development, abnormal of barnacles, 116; of tunicates, 215
 Development and fecundity of flour beetles, 368
 Dial gauge dendrometers, note, 208
 Dice, Lee R., note, 389-391
 Distribution, vertical of phytoplankton and the thermocline, 386
 Dobzhansky, Th., review, 219
 Driftless area of southwestern Wisconsin, relation of soils and forest growth, 173-180

E

- Eaton, Richard, book notice, 225
 Ecological segregation of inter-fertile species of *Colias*, article, 461
 Ecological succession of spiders of the Chicago area dunes, article, 334-351
 Ecology, method in—biopocrosis, 30-42
 Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California, article, 242-253
 Ecology of fungi, survey of literature, 376-382
 Edwards, John P., co-author, article, 360
 Eggler, Willis A., article, 415
 Egler, Frank E., note, 382-386
Eleocharis macrostachya, colonization on an open shoal, 205-208
 Emlen, John T., Jr., Allen W. Stokes, and Charles P. Winsor, article, 133-145
Encarsia formosa, 181

F

- Fat content of a butterfly, *Danaus plexippus* Linn., as affected by migration, article, 80-94
 Fecundity and development of flour beetles, article, 368-374
 Fern, Polypody, water relations, 43-53
 Fish populations, variations in size and composition in recently stocked ponds, 401
 Fishes of the Great Lakes region, book review, 222
 Fletcher, Joel E., and W. P. Martin, article, 95-100
 Flood, effect on animals, 505
 Fog and atmospheric carbon dioxide as related to apparent photosynthetic rate of some broadleaf evergreens, note, 507
 Forage, production of, resulting from grazing lowland prairie, 1-29

- Forest growth and soils in the driftless area of southwestern Wisconsin, 173-180
 Forest sequence and climatic change in north-eastern North America since early Wisconsin time, article, 326-333
 Forests of Itasca Park region, Minnesota, life-form spectra, 352-359
 Forests, postglacial, of Glacier National Park region, 146-152
Formica, comparison of two ants of the genus, 316
 France, hardpan development in Landes region, 375-376
 Frank, Marian Burton, co-author, article, 368
 Frequency index and population density, 389
 Fungus sociology and ecology, survey of literature, 376-382

G

- Gates, Frank C., note, 205-208
 Genus *Formica*, comparison of two, 316
 Georgia, fog and carbon dioxide as related to photosynthetic rate of broadleaf evergreens, 507
 Germination of desert plants in Joshua Tree National Monument, California, 242-253
 Gessner, Fritz, note, 386-389
 Glacier National Park, postglacial forests, 146-152
 Glaessner, Martin F., book notice, 225
 Goldenrod community, phytosociological analysis, 124-125
 Grass, as indicator of condition of southwestern mixed grass ranges, 190-204
 Grassland types of south central Montana, article, 449
 Grazing lowland prairie, changes in vegetation and production of forage, 1-29
 Greenhouse whitefly, modal temperatures, 181
 Growth of barnacles, 116
 Gustafson, A. F., reviewed, 524

H

- Hansen, H. P., article, 146-152; review, 398-399
 Hardpan development in the Landes region of France, note, 375-376
 Heady, Harold F., note, 519
 Hormones and behaviour, book review, 396
 Hovanitz, William, article, 461
 Hubbs, Carl L., and Karl F. Lagler, reviewed, 222
 Humes, Arthur J., note, 392
 Huntsman, A. G., article, 30-42

I

- Indicator value of perennial grass composition of southwestern mixed grass ranges, 190-204
 Instruments and methods, microclimatic, review, 223-224
 Itasca Park region, Minnesota, life-form spectra of hardwood forests, 352-359

J

- Jacobs, Don L., book notice by, 225
Joshua Tree National Monument, California,
germination of desert plants, 242-253

K

- Kashkarov, D. N., reviewed, 394
Kendeigh, S. Charles, article, 101-114
Kinsey, Alfred C., Wardell B. Pomeroy, and
Clyde E. Martin, reviewed, 522
Krumholz, Louis A., article, 401
Krutzsch, Philip, note, 391
Küchler, A. W., note, 513

L

- Lack, D., reviewed, 219
Lake Erie, temporary changes of limnological
conditions produced by a windstorm, 501
Larval coleoptera and diptera from marine crus-
taceans, note, 392
Latin America, plants and plant science, review,
400
Latrodectus revivensis sp. nov. from Palestine,
note, 209-215
Lemna minor as an aggressive weed in the Sud-
bury River, book notice, 225
Life-form spectra of the hardwood forests of the
Itasca Park region, Minnesota, article, 352-
359
Limnological conditions, temporary changes in
western Lake Erie produced by a wind-
storm, 501
Lindsey, Alton A., article, 470
Livingston, Burton E., article, 227-241
Logs, fallen, plant succession in virgin spruce-fir
forest, 508
Louisiana, phytosociological analysis of golden-
rod community, 124-125
Louisiana, water relations of polypody fern, 43-
53
Lowman, S. W., book notice, 225
Lowrie, D. C., article, 334-351
Lull, R. S., book notice, 131

M

- Mammals of North America, book review, 129
Mammals of Washington State, review, 525
Manchuria, new vegetation map, 513
Marine organisms, seasonal occurrence of, 153
Marine zooplankton, nutritional value of, 54
Martin, Clyde E., co-author, reviewed, 522
Martin, S. Clark, note, 393
Martin, W. P., co-author, article, 95-100
Maryland, survival of wild brown rats on a
farm, 437
Mason, Ralph S., note, 125-126
Mather, K., reviewed, 130
McCullough, Herbert A., note, 508
Merrilleana, review, 521
Mesquite seeds remain viable after 44 years,
note, 393

- Method in ecology—biapocrisis, article, 30
Method of obtaining undisturbed soil samples,
125-126
Methods and instruments, microclimatic, review,
223-224
Mexico, plant communities in the vicinity of the
volcano El Parícutin after two and a half
years of eruption, 415
Michigan, bird populations and biotic communi-
ties in, 101
Michigan, changes of limnological conditions in
western Lake Erie produced by a wind-
storm, 501
Michigan, colonization of certain aquatic plants
on an open shoal, 205-208
Michigan, Sodon Lake, sequence of pollen spec-
tra, Profile I, 492
Microclimatic instruments and methods, an an-
notated bibliography, review, 223-224
Micropaleontology, principles, book notice, 225
Migration of a butterfly, fat content as affected
by, 80
Miller, Robert R., review, 222
Minnesota, life-form spectra of hardwood forests
of Itasca Park region, 352-359
Minnesota, Pleistocene flora, 284-315
Modal temperatures for the greenhouse whitefly,
... , article, 181-189
Molds, effects of, in rain-crust of desert soils,
95-100
Montana, postglacial forests, 146-152
Montana, south central, grassland types, 449
Montgomery, R. B., and co-authors, reviewed,
128
Moore, Carl R., review, 396

N

- Nebraska, results of grazing lowland prairie,
1-29
New method of obtaining undisturbed soil sam-
ples, note, 125-126
New Mexico, terron vegetation, 470
New vegetation map of Manchuria, note, 513
Newcombe, Curtis L., review, 524
Newman, H. H., review, 397
Northeastern North America, forest sequence
and climatic change since early Wisconsin
time, 326-333
Nutritional value of marine zooplankton with
consideration of its use as an emergency
food, article, 54-71

O

- Observations on a population of the salamander,
Amphiuma tridactylum Cuvier, article, 479
Observations on the abnormal development and
growth of barnacles as related to surface
toxicity, note, 116-119
Observations on the effect of flood on animals,
note, 505
Occurrence of marine organisms in Biscayne
Bay, Florida, 153

Ohio, changes of limnological conditions in western Lake Erie produced by a windstorm, 501

Organisms, marine, seasonal occurrence, 153

Oxygen tension, toleration by crayfish, 360

P

Palestine, *Latrodectus revivensis* sp. nov. from, 209

Palynological studies at Sodon Lake, Michigan. Part III. The sequence of pollen spectra, Profile I, article, 492

Paricutin volcano, plant communities in vicinity after two and a half years of eruption, 415

Park, Thomas, and Marian Burton Frank, article, 368-374

Penfound, Wm. T., co-author, article, 43-53; note, 124-125

Perennial grass composition as an indicator of condition of southwestern mixed grass ranges, article, 190-204

Photosynthetic rate of broadleaf evergreens as related to fog and carbon dioxide, 507

Phytoplankton and the thermocline, distribution of, 386

Phytosociological analysis of a goldenrod community near Kenner, Louisiana, note, 124-125

Phytosociological research, use of punched card method, 516

Plant communities in the vicinity of the volcano El Paricutin, Mexico, after two and a half years of eruption, article, 415

Plant succession on fallen logs in a virgin spruce-fir forest, note, 508

Plants and environment: a textbook of plant autecology, review, 398-399

Plants and plant science in Latin America, review, 400

Pleistocene flora of Minnesota, 284-315

Pollen spectra sequence, Profile I, at Sodon Lake, Michigan, 492

Polypodium polypodioides (L.) A. S. Hitchcock, water relations, 43-53

Pomeroy, Wardell B., co-author, reviewed, 522

Ponds, recently stocked, variations in size and composition of fish populations, 401

Population density, relationship between frequency index and, 389

Population of the salamander, *Amphiuma tridactylum*, 479

Populations, bird, and biotic communities, 101

Populations, fish, variations in size and composition in recently stocked ponds, 401

Populations, rate of recovery of brown rats in nature, 133

Postglacial forests of the Glacier National Park region, article, 146-152

Potts, Roberta, and Wm. T. Penfound, article, 43-53

Prairie lowland, changes in vegetation and production of forage resulting from grazing, 1-29

Preston, F. W., note, 115-116; article, 254-283
Principles of micropalaeontology, book notice, 225

Punched card method in phytosociological research, 516

R

Rain-crust of desert soils, effects of algae and molds, 95-100

Range condition as indicated by perennial grass composition, 190-204

Range management and annual-plant vegetation of the California foothills, 72-79

Range society formed, note, 519

Rarity, and commonness of species, 254

Rashevsky, N., review, 394

Rate of recovery of decimated populations of brown rats in nature, article, 133-145

Rats, recovery of decimated populations, 133

Rats, wild brown, survival on a Maryland farm, 437

Rattus norvegicus, 133

Recent clastic sediments project, book notice, 225

Recovery of populations of brown rats, 133

Reineke, Lester H., note, 208

Relation of soils and forest growth in the driftless area of southwestern Wisconsin, article, 173-180

Relationship between frequency index and population density, note, 389-391

Rosendahl, C. O., article, 284-315

Rosenthal, G. M., Jr., review, 128

Russian textbook of ecology, book review, 394

S

Salamander, *Amphiuma tridactylum*, observations on a population, 479

Sanborn, Colin Campbell, reviews, 129, 525

Schmidt, Karl P., review, 221

Scientists starred, 1903-1943, book review, 397

Scirpus acutus, colonization on an open shoal, 205-208

Sears, Paul B., article, 326-333

Seasonal occurrence of sedentary marine organisms in Biscayne Bay, Florida, article, 153-172

Sediments, recent clastic, book notice, 225

Seeds of mesquite viable after 44 years, 393

Shulov, S., note, 209-215

Sisam, J. W. B., reviewed, 222-223

Slater, J. V., co-author, article, 492

Soil samples, new method of obtaining undisturbed, 125-126

Soils and forest growth in the driftless area of southwestern Wisconsin, 173-180

Soils, desert, effects of algae and molds in rain-crust, 95-100

Solidago hirsutissima, phytosociological analysis of community, 124-125

Some conversational autobiographical notes on intellectual experiences and development: an auto-obituary, article, 227-241

Some effects of algae and molds in the rain-crust of desert soils, article, 95-100

Species, commonness and rarity, 254

Spiders, ecological succession in dunes area, Chicago, 334

Spurr, Stephen H., review, 222-223

Statistical analysis in biology, book review, 130

Stickel, Lucille F., note, 505

Stokes, Allen W., co-author, article, 133-145

Strong, Reuben Myron, book notice, 131

Succession, ecological, of spiders in the Chicago dunes area, 334

Succession, plant, on fallen logs, in virgin spruce-fir forest, 508

Survey, aerial, in forestry and agriculture, review, 222-223

Survey of literature on fungus sociology and ecology, note, 376-382

Survival of wild brown rats on a Maryland farm, article, 437

Swain, Fred M., book notices by, 225

T

Talbot, M. W., co-author, article, 72-79

Talbot, Mary, article, 316-325

Temperatures constant, fecundity and development of flour beetles, 368

Temporary changes of certain limnological conditions in western Lake Erie produced by a windstorm, note, 501

Terron vegetation in New Mexico, article, 470

Thermocline and distribution of phytoplankton, 386

Toleration of lowered oxygen tension by cave and stream crayfish, article, 360-367

Toxicity, surface, as related to growth and development of barnacles, 116

Trialeurodes vaporariorum and its parasite *Encarsia formosa*, modal temperatures for, 181

Tribolium confusum and *Tribolium castaneum*, fecundity and development of, 368

Tunicates, abnormal development of, 215

2,4-D effects in Connecticut vegetation, 1947, note, 382-386

U

United States, conservation, 524

Use of aerial survey in forestry and agriculture, review, 222-223

Use of punched card method in phytosociological research, note, 516

V

Value, nutritional of marine zooplankton, 54

Variations in size and composition of fish populations in recently stocked ponds, article, 401

Vegetation changes resulting from grazing lowland prairie, 1-29

Vegetation, effects of 2,4-D in Connecticut, 1947, 382-386

Vegetation map of Manchuria, 513

Vegetation of the California foothills as related to range management, 72-79

Vegetation, terron, New Mexico, 470

Verdoorn, Frans, editor, reviewed, 400, 521

Vertical distribution of phytoplankton and the thermocline, note, 386-389

Viability of mesquite seeds after 44 years, 393

Visher, Stephen Sargent, reviewed, 397

Vogt, William, reviewed, 221

Volcano El Paricutin, plant communities in vicinity after two and a half years of eruption, 415

W

Washington State, mammals, 525

Water relations of the Polypody fern, *Polypodium polypodioides* (L.) A. S. Hitchcock, article, 43-53

Water-like surfaces attract volant desert animals, note, 391

Weaver, J. E., and R. W. Darland, article, 1-29

Weiss, Charles M., notes, 116-119, 215-218; article, 153-172

Went, F. W., article, 242-253

Whitford, Philip B., co-author, article, 173-180

Wilbur, Robert L., co-author, article, 352-359

Wilde, S. A., Philip B. Whitford, and C. T. Youngberg, article, 173-180

Wilson, C. C., note, 507

Windstorm, temporary changes of limnological conditions in western Lake Erie, 501

Winsor, Charles P., co-author, article, 133-145

Wisconsin, relation of soils and forest growth in the driftless area, 173-180

Wisconsin time to present, forest sequence and climatic change in northeastern North America, 326-333

Woods, Loren P., review, 222

Wright, Elnora A., co-author, article, 449

Wright, John C., article, 449

Y

Youngberg, C. T., co-author, article, 173-180

Z

Zooplankton, marine, nutritional value of, 54

I. A. R. I. 75.

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